A POPULATION BIOLOGY OF BREEDING REDSHANKS

(*Tringa totanus* L.)

by

BARRY JOHN YATES.

A thesis submitted in part fulfilment of the requirements for the degree of Doctor of Philosophy of the Council for National Academic Awards.

Department of Biology
Liverpool Polytechnic
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ABSTRACT.

A breeding population of Redshanks was studied by trapping adults at the nest and individually marking them, over a period of nine years, on part of the extensive Ribble saltmarshes. Other aspects of breeding biology were investigated over three years.

The capture-recapture analysis of the breeding adults revealed an overall annual survival rate, of both sexes, of 0.77, and a population of approximately 200 pairs in 1.04km^2.

Mate fidelity was very high, with 71% of surviving pairs remaining faithful. Nest site fidelity was extremely strong for faithful pairs and males with new mates, but significantly weaker for females with new mates. A lower nest site fidelity of young birds was regarded as a major contributing factor to their lower recapture rates.

The timing of both the onset and ending of the breeding seasons varied greatly, and was determined mainly by the rainfall. High rainfall delayed onset and hastened ending of breeding. Within a breeding season the older birds bred throughout, while the young ones were mostly not able to breed early.

The substantial losses of nests due to cattle grazing on the marsh (45%) could easily be controlled by preventing the access of cattle to the main breeding area until after the end of the nesting season. Nest predation was rare (less than 4%) in most years, but increased in a year of short vegetation (to 25%). The production of pulli was estimated under varying environmental influences and ranged from 0.73 to 2.28 pulli.pair^{-1}.

The variation of egg size within the population was investigated and the significant influences of laying order (within a clutch) and maternal size demonstrated. Pullus size at hatching was positively correlated with egg size and also with maternal size.

The growth and development of pulli were described for weight, bill length, tarsus length and postnatal moult. For three days after hatching the weight remained below the hatching value and then rapidly increased, whereas the bill and tarsus showed a linear increase in length

A tentative model of the population dynamics was produced, despite the lack of good estimates of pre- and post-fledging mortality. This model indicated a high pre-fledging mortality of 0.67 and also further highlighted the impact on the population of cattle grazing during the nesting season.

ACKNOWLEDGEMENTS.

The Nature Conservancy Council enabled this study to continue after the threatened recla mation of the area, and co-operated with the requirements of this study.

For the collection of much of the mass of data from 1973 to 1981 I am greatly indebted to the expertise and persistent enthusiasm of Mr. M.J. Greenwood. For this, and his constant encouragement during the last three years, I thank him. The contributions by the previous workers of this study, Dr. M.E.Greenhalgh and Dr. R.A. Ashcroft, are also thankfully acknowledged. Professor W.G. Hale initiated and supervised this study, and provided facilities for me within the Biology Department, Liverpool Polytechnic. Dr. C.J. Feare made sufficient constructive criticism to benefit this thesis, yet maintain my enthusiasm to the completion of this work.

Problems I had with statistical analyses were clearly explained and solved by Mr. J. Higgins of the Mathematics Department, Liverpool Polytechnic, and in the analysis of the capture-recapture data I was aided by Dr. M.V. Hounsome of Manchester Museum.

Finally, my effort in this study, especially during the months of fieldwork, could not have been so great without the support and encouragement of my wife, Anne.

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C O N T E N T S .

CHAPTER THREE - THE ADULTS

CHAPTER FOUR - THE EGGS

CHAPTER ONE - INTRODUCTION.

1.1 General Introduction.

Many aspects of avian ecology can be investigated by the intensive study of a single species during the breeding period within a defined area. The most important of these are the components of the dynamics of the population; assessing the production & determining the losses throughout the life cycle. With detailed records kept from year to year it is also possible to determine the degree of nest site and mate fidelity. In addition, other aspects of the breeding biology can be described, such as egg size, pullus growth and adult size, together with their interrelationships.

The extent and quality of the results obtained are largely determined by the species chosen and the study site. The character--istics of a species that contribute to the extent of a study include;

a) strong nest site fidelity - enabling the same individuals to be studied over several years, creating a more or less spatially stable population.

b) a well defined, isolated study area - giving a clear definition of the population.

c) an easily studied species - such that nest sites are easily discovered and accessible, and the individuals tolerant of capture and observation.

Amongst the birds there are many 'suitable' species (for example the Great Tit Parus major , which has been so intensively studied by many workers), but a large group, the sub-order Charadrii, is in general difficult, and has been much neglected during the breeding season.

The majority of species within the Charadrii can be termed

waders, or shorebirds, and the largest family, the Scolopacidae, contains eighty-five species of sandpipers, snipes and phalaropes. These typically breed in remote places, often in the arctic, usually at low densities, and therefore, long detailed studies of this group are few in number.

The Redshank is a medium sized to large Tringine sandpiper, that breeds in wet grassland throughout Western and Central Europe and eastwards into Asia (Hale, 1971). At the study site it can be studied with some difficulty as it partially satifies the above ideal characteristics. As will be seen the adults (especially the males) are highly site faithful, which means that despite the study area being only part of a much larger area of suitable habitat, the population is well defined. As a result of the high density of pairs ($200 pairs.km^{-2}$ - see Section 3.3.7), and if enough effort is expended, many nests can be found, which provide ample scope for study. The adults are easily captured at the nest and their eggs and pulli can be marked and measured, enabling many relationships to be determined.

However, after leaving the nest the family parties are difficult to observe critically at this site, so that many vitally important aspects of breeding biology and population dynamics (such as, the effect of climate on growth and pre-fledging mortality, the average pre-fledging mortality and the mortality up to the age of first breeding) were not investigated. In addition, other questions that could be answered at this site, such as, the adult energetics during the breeding season, pullus energetics and the occurrence of non-breeders, have not been investigated because of the lack of time.

The Redshank has increased its breeding distribution (and population level) in the British Isles during the past hundred years

(Thomas, 1942), but now much of its breeding habitat is threatened by drainage and land reclamation schemes (see Langslow 1981, for coastal sites, and Caufield 1981, for inland sites). The Redshank is, therefore, threatened by man's activities, and its present high level of population cannot be maintained.

In his reveiw of mortality and fertility of waders Boyd (1962) concluded;

"If measures of conservation are to gain support, it is essential that much more should be learned about the inherent characteristics of wader populations, so that the likely outcome of proposed changes in legislation of land use can be predicted correctly more often than not.

The most fruitful approach to the dynamics of wader populations seems to be by concentration on long-term observations of breeding groups. The especial need is for careful breeding censuses, including determinations of the numbers of young fledged, coupled with marking to deal with the problems of emigration, immigration and the age of maturity."

However, Watson (1973) considered that "... to do research on population dynamics in birds is not easy" and in the Redshank this is certainly true.

1.2 The Study Site.

This study was carried out within the Banks Marsh N.N.R. , on the Ribble Estuary, located at 53°42' N 02°57' W , and lying between Southport and Preston, in Lancashire, N.W. England (see Fig. 1.1).

The estuary holds large, non-breeding populations of waders throughout the year (Smith and Greenhalgh, 1977), as well as a large exploited population of wintering wildfowl. In addition there is a diverse breeding bird community (Greenhalgh, 1971), that is continually changing due to land reclamation schemes, pressures from grazing and the maturing of the saltmarsh. During my period of study, Banks Marsh supported the following, approximate populations of breeding birds (Jones, 1980);

Black-headed Gull (*Larus ridibundus*) - 6,000 pairs.

Lesser Black-backed (*L. fuscus*) and Herring Gulls (*L. argentatus*) - - 700 pairs.

Common Tern (*Sterna hirundo*) - 300 pairs.

Oystercatcher (*Haematopus ostralegus*) - 6 pairs.

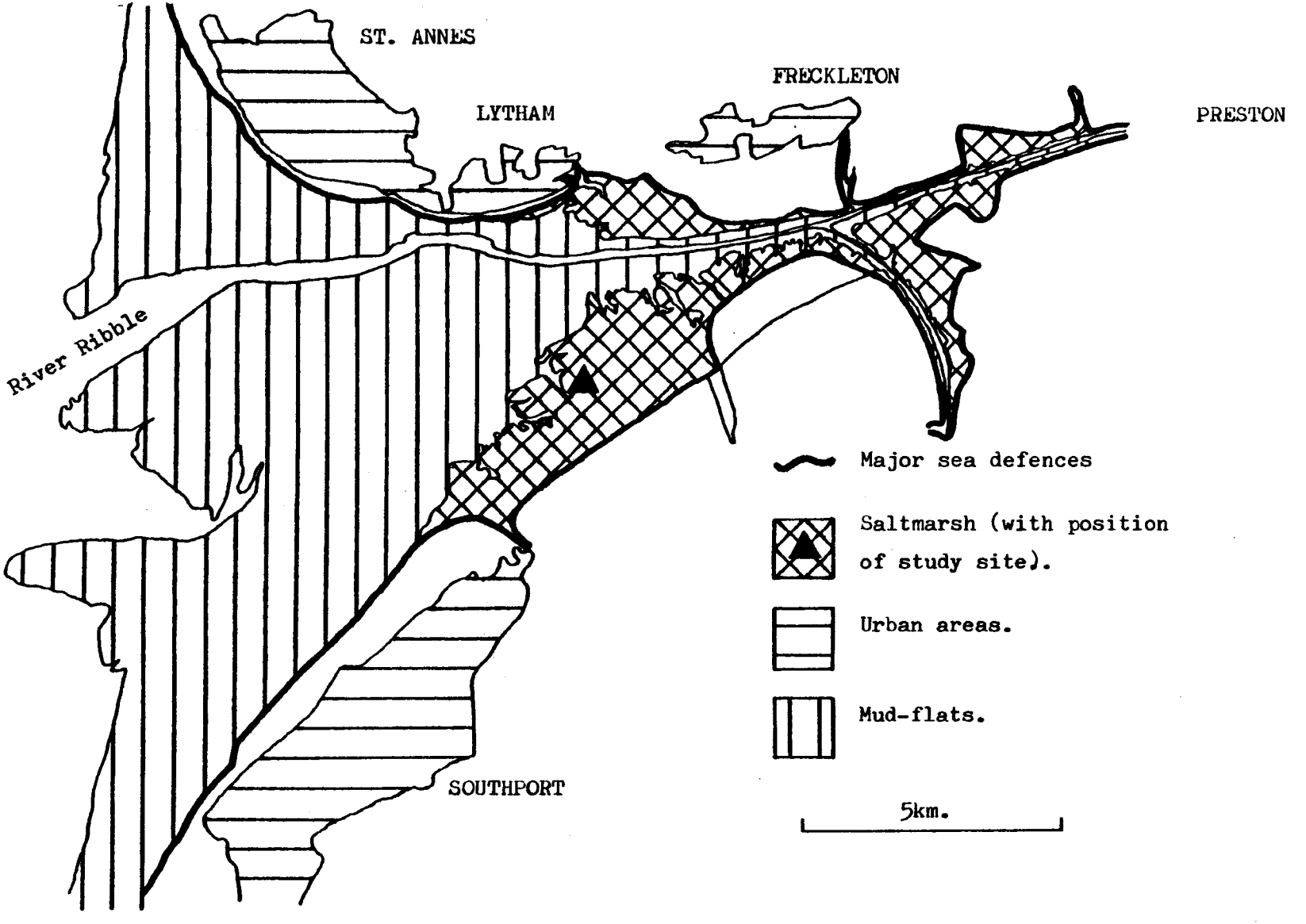
Skylark (*Alauda arvensis*) and Meadow Pipit (*Anthus pratensis*) - numerous but not counted.

plus of course , the numerous Redshanks.

Banks Marsh is bounded on the landward side by an embankment 4 to 5m. high, that was constructed to protect the land, and which has aided the development of the saltmarsh from the mud-flats. Now the mud-flats are found on the seaward side of the saltmarsh, some 2km. away (for a full account of this reclamation see Gresswell, 1953).

The vegetation varies generally with the height of the saltmarsh, with *Festuca rubra* growing on the high areas, *Puccinellia maritima* on the lower areas, and *Spartina anglica* on the very low

Fig. 1.1 The Ribble Estuary



areas that are regularly covered by the tide. Within the study area the distribution of these vegetation types is shown in Fig. 2.4(b). The high areas of Festuca rubra are only covered by the very highest tides, and it is here that most of the Redshanks nest.

The saltmarsh is grazed annually by cattle from May until October, and so during most of the breeding season they pose a threat to nests. This threat, of crushing the nests, is great (see Section 2.3.4), and also hindered the nest trapping, so some areas were fenced off from the cattle until the beginning of July, when most of the Redshank had finished nesting (see Fig. 2.1).

During the cold winter of 1978-79 the saltmarsh was heavily grazed by sheep, and this resulted in a very short vegetation throughout the following breeding season.

The total area covered by the study represents some 2km.^{2} of Banks Marsh, but the Restricted Area of 1.04km.^{2} (see Section 2.3.1) was the main area of interest, and this is shown in Fig. 2.3 .

1.3 Previous Work On The Redshank At This Study Site.

In 1970 the distribution of wader nest sites on Banks Marsh was mapped, and the density of pairs estimated; for the Redshank this was 22.5 pairs.km.$^{-2}$ (Greenhalgh,1971). This work was referred to by Sharrock (1976), and is, therefore, widely quoted.

However, in 1973 the trapping of breeding adults began in the area of this study, and with the consequent increase in effort spent searching for nests many more were found than by Greenhalgh (1971). During the following two years the effort was further increased, although nest searching and trapping were still largely carried out part-time, and the number of nests found similarly increased.

The period from 1976 to 1978 saw the first full-time work, with the studentship of R.P. Ashcroft, being assisted in the field by M.J. Greenwood.

Throughout the nine years from 1973 the work was supervised by Professor W.G. Hale.

The results obtained were reported by Ashcroft (1978). These concentrated on breeding behaviour and contained little detailed analysis such that some of the summaries are of a spurious nature (see especially summaries 18,24,27,31,32,43 and44). In addition, measurements derived from the map (for example, distances between nests, density estimates and movements of broods) are inaccurate, because an area assumed to be 100ha. on the map was measured, and found to be only 68ha. The results of Ashcroft (1978), where relevant to the present study, are compared and discussed in each chapter.

1.4 The Aims Of The Study.

Initially the capturing, ringing and measuring of breeding Redshanks at this site had few specific aims, other than to build up a history of the individuals known to be breeding, providing the potential for future study. The position of nests was mapped and records of the adults caught and the nesting success kept. After six years of work it was considered there was still the potential for fruitful research, and I was given the task of determining the methods and carrying them out.

Within the restrictions of the 'traditional' trapping regime I realised that additional measurements could be made of the eggs and pulli, which would provide me with new avenues of study.

The main aims of this study were to describe the losses at different stages of the life cycle, and relate these to the production. The estimation of adult mortality could potentially be made over the full nine years of the project, and as such would represent a long term study, as suggested by Boyd (1962). The losses during the incubation period could also be easily measured and sub-divided, then considered with respect to vegetation influences. However, the estimation of losses after hatching, until the age of first breeding was considered too time consuming to be attempted within this study. The extreme mobility and elusiveness of the species would necessitate a separate study for the determination of this very important aspect of the dynamics of the population.

It became obvious that there was a major drawback to studying the Redshank, and this was the difficulty of determining the sex of an individual. There was no established method acceptable to me, and without one there could have been no detailed study. The regime

developed in this study for sexing individuals is considered accurate enough for this extensive study, and full details are given in Section 3.2.2 . Following this it was possible to investigate the sex differences of body size, annual survival, population size, mate and nest site fidelity, and further, relate adult (maternal) body size to that of the eggs and pulli.

An attempt to investigate the development of pulli was made, and even though the daily samples were small, the satisfactory results justified the great effort made in capturing each pullus.

As a result of some of the above major aims many data were collected that enabled other investigations to be considered, and these included the movements of adults outside the breeding season, and the movements of pulli during the pre-fledging period.

1.5 The Relation Of This Study To Others Of Waders.

Detailed investigations, comparable with this study have been made on several wader populations, for example, Dunlin (*Calidris alpina* , by Soikkeli, 1967 and 1970), Red-necked Phalarope (*Phalaropus lobatus* , by Hilden, 1972) and Temminck's Stint (*Calidris temminckii*, by Hilden, 1978). In these studies the use of long lasting, individually numbered leg rings was essential to follow individuals from nest to nest, and from year to year. Where comparisons could be made with the results of the present study they are discussed in the relevant chapters.

A major study of the Redshank by Grosskopf (1958 et seq.) deserves special mention here. Started in 1955, this study was one of the first long term studies of a breeding population of a wader. Initially it was based on just ringing as many breeding individuals as was possible, but it quickly developed into a more detailed investigation, that resulted in much new information on this species.

The study attempted to cover most aspects of the breeding biology of the Redshank, but in doing so many of his samples were small and his conclusions largely subjective, with little analysis to enforce his claims. This approach was satisfactory for his detailed descriptions of behaviour, but mostly inadequate for the more quantitative aspects of the study. These latter aspects included the determination of nest site and mate fidelity, and the mortality estimates. Despite these shortcomings, his study provided a good comparison for this study, which overall, showed good general agreement.

CHAPTER TWO - THE NESTS.

2.1 INTRODUCTION.

This chapter clearly defines the main study area, and describes the spatial distribution of nests within it. The temporal distribution of nests is also investigated, firstly, within a season, by the frequency distribution of clutch completion dates, and secondly, between seasons, by attempting to explain the onset and ending of breeding in terms of the meteorological conditions prevailing.

The nest losses are categorised, with each being estimated, then considered with respect to changes in environmental factors, such as, tides, grazing pressure, predators, and the adult trapping regime.

Finally, the overall production of pulli is estimated, under the influence of different environmental factors.

2.2 METHODS

2.2.1 Finding, Mapping and Marking the Nests.

The nests were always found on the ground, usually within a grassy tussock, and concealed. Before the clutch was completed, or in short vegetation, the eggs were sometimes visible, but due to their cryptic patterning, and colouration, were not often conspicuous. It follows, that finding the nests within the study area took up much of the available time during the annual study period.

Three methods of search were employed, and these were ranked in order of decreasing success;

a) Active Search - walking around all of the study area, looking for the clues that indicated the prescence of a nest. These included, tussocks with dark, hollow interiors, runs and/or entrances, and most useful of all, the 'bower effect' in the vegetation, caused by the incubating birds bending the vegetation over the nest. Another factor localising the search was the discovery of 'scrapes', made by the male of the pair, which were often associated with the actual nest.

b) Flushing - some individuals could be approached quite closely during incubation, so that when they left the nest, with a characteristically low flight, it could be pinpointed. This method worked best in bad weather and/or with a nest close to hatching, and if the approach was made from downwind, when birds could be flushed at close range.

c) Passive Search - by sitting in a hide, or at a great distance from an area, a watch could be kept for birds returning

to incubate, and then, by reference to local landmarks, the nest could often be found.

Searching within a day was not consistent over the study area, but during several days the total area was covered.

Once found the nests could easily be lost again, so a discrete marker was placed 10 m. from the nest in a specified direction. This was not exploited by predators.

The position of the nest was found on the map by one of two means. If a distinctive channel was nearby the position could be accurately determined. However, in a uniform area, with few distinctive landmarks, the position was determined by triangulation, using a sighting compass, and large posts positioned accurately within the study area.

2.2.2 The Determination of Nest Losses.

From the regular visits to the nests it was possible to categorise the cause of loss, or extent of success, as well as the timing of events, for each nest.

Nine catagories of outcome were identified;

a) Uncompleted - a partial clutch (usually a single egg), that had not been incubated (as determined by flotation, see later).

b) Hatched - at least one chick successfully hatched.

c) Deserted - an end to incubation, with the clutch still present, and no distinct causal factor.

d) Predation loss - at least one egg removed by a predator that resulted in desertion.

e) Flooded - the inundation of the clutch by a high tide, that caused clutch loss or desertion.

f) Crushed - at least one egg damaged by cattle, that

resulted in desertion.

g) Addled - the extended incubation of a clutch, caused by the failure of any egg to hatch, or, the bursting of an addled egg, causing desertion.

h) Trapping loss - desertion immediately following the trapping at a nest.

i) Old - a nest found after the date of outcome.

The recording of nest loss was undertaken with great care, and the distinguishing of the real and apparent causes was often possible, because of the frequent nest visits. For example, a visit to a nest may have indicated desertion (eggs cold), and a subsequent visit may have followed a high tide that flooded the clutch. The outcome of the nest would have been recorded as desertion, but this distinction was only possible because of the intermediate visit.

In addition to the fate of nests, the fate of individual eggs, from nests completing their full incubation period, was noted.

2.2.3. The Vegetation Surveys.

Two coarse assessments of the vegetation were made, to compare with the distribution of nests.

a) Annual survey of vegetation height on 1st. April - in the years 1979 - 81 the same eighteen random points were located in the study area, and, at each, six random measurements of the height of the vegetation were taken. The mean of these values was used as an indicator of the height of the vegetation at the same date each year.

b) Distribution of *Spartina anglica* and *Festuca rubra*, in July 1980 - this survey mapped these two distinct vegetation types on to the standard field map, using the location of channels, or

triangulation methods. The intermediate areas were dominated by Puccinellia maritima. This is shown in Fig. 2.4

Such a large scale survey was only possible because of the abscence of grazing. This allowed the dominant vegetation of Festuca rubra to flower and ripen in continuous stands that could be easily mapped.

2.2.4 Fenced Areas.

Nests sited on grazed saltmarsh had a great chance of being crushed (see Section 2.3.4), and, in addition, the cattle were attracted to the nest traps, often disturbing the birds within. The combined effect of these was that some nests were deserted before the pair was captured, and the data on most nests were , therefore, incomplete.

To overcome this inefficiency, various fences were constructed to exclude the cattle, and these are shown in Fig. 2.1.The fences from 1977 to 1979 were of barbed wire and posts, while the fence of 1980 - 81 was an electric one, over 800 m. long, that joined two large channels, and thereby excluded cattle from the entire study area.

2.2.5 Meteorological Data.

Details of the weather during the period of study were obtained from the records of the Meteorological Office at Blackpool Airport, 12 km. to the north of the study area. The data were of four daily measurements;

a) maximum daily air temperature (°C).

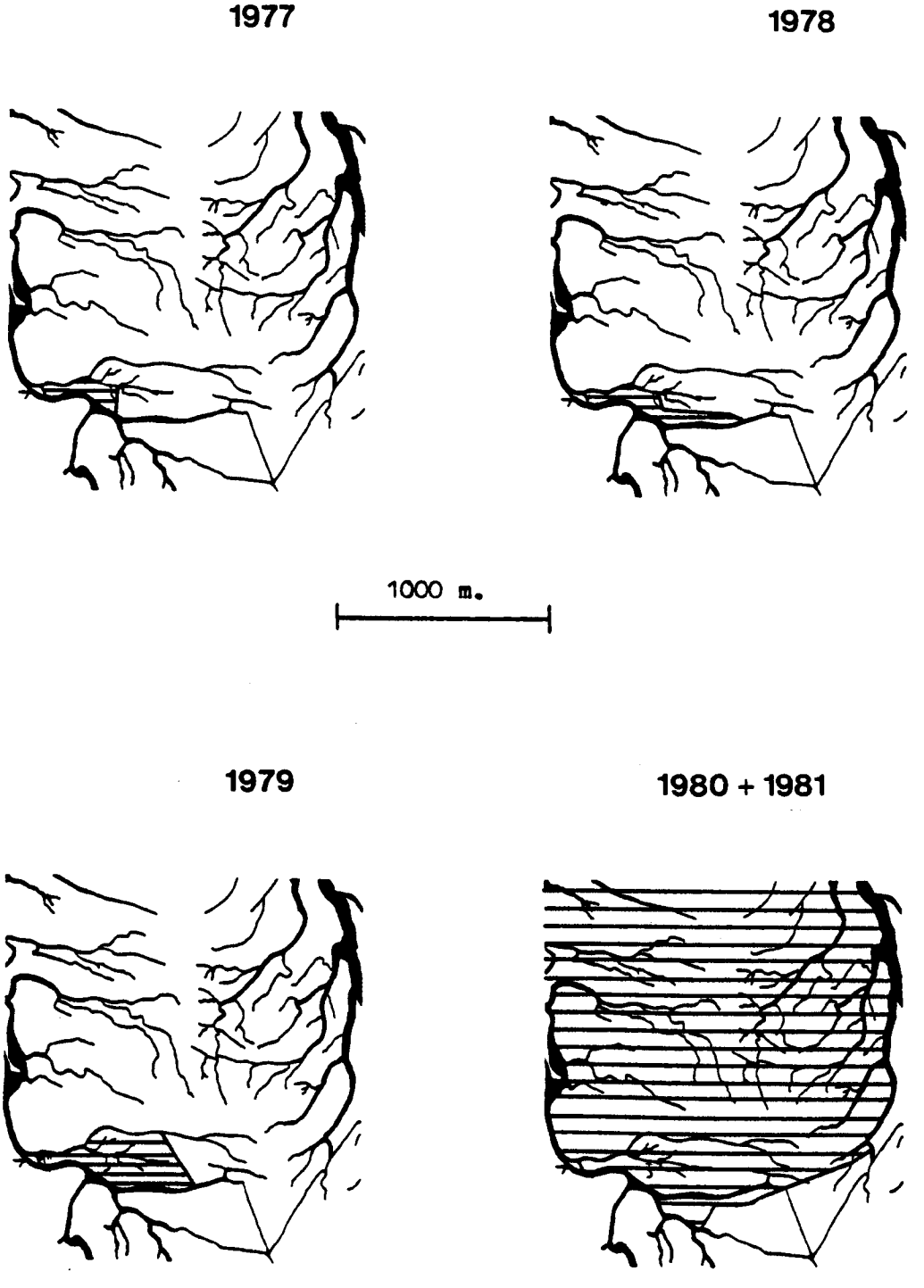
b) minimum daily air temperature (°C).

c) mean daily windspeed (knots).

d) total daily rainfall (mm.).

Fig. 2.1 The Fenced Areas, 1977 to 1981.

The shaded areas were protected from cattle.



2.3 RESULTS.

2.3.1 The Restricted Area.

The areas in which nests were found each year, is shown in Fig. 2.2, and it was seen that there had been much variation. This was considered to be due to an inconsistent effort, especially noticeable in the early years of the study. As a result, many problems were introduced into the estimation of adult mortality, and population size (see Section 3.3), such that it was necessary to delimit an area in which there had been similar effort in nest finding each year. Retrospectively, this was only possible by considering the maps of the nests found.

The 1973 season was excluded, because of the small area covered, and the area covered by all other seasons nests in every season was used as the basis for the Restricted Area. An extra fifty metres was added to the perimeter, since nest searching would have extended past the last nest found, except at natural boundaries (that is the large channels). This represented an area of saltmarsh of 1.04 $km.^2$ and it is shown in Fig. 2.3.

The Restricted Area also excluded the continuous stands of Spartina anglica , in which the nest finding efficiency was considered to be low. Fig. 2.4 showed the main vegetation of the saltmarsh.

Fig. 2.2 The Areas in Which Nests Were Found, 1973 to 1980.

The shaded polygons were produced, for each separate season, by joining the outermost nests.

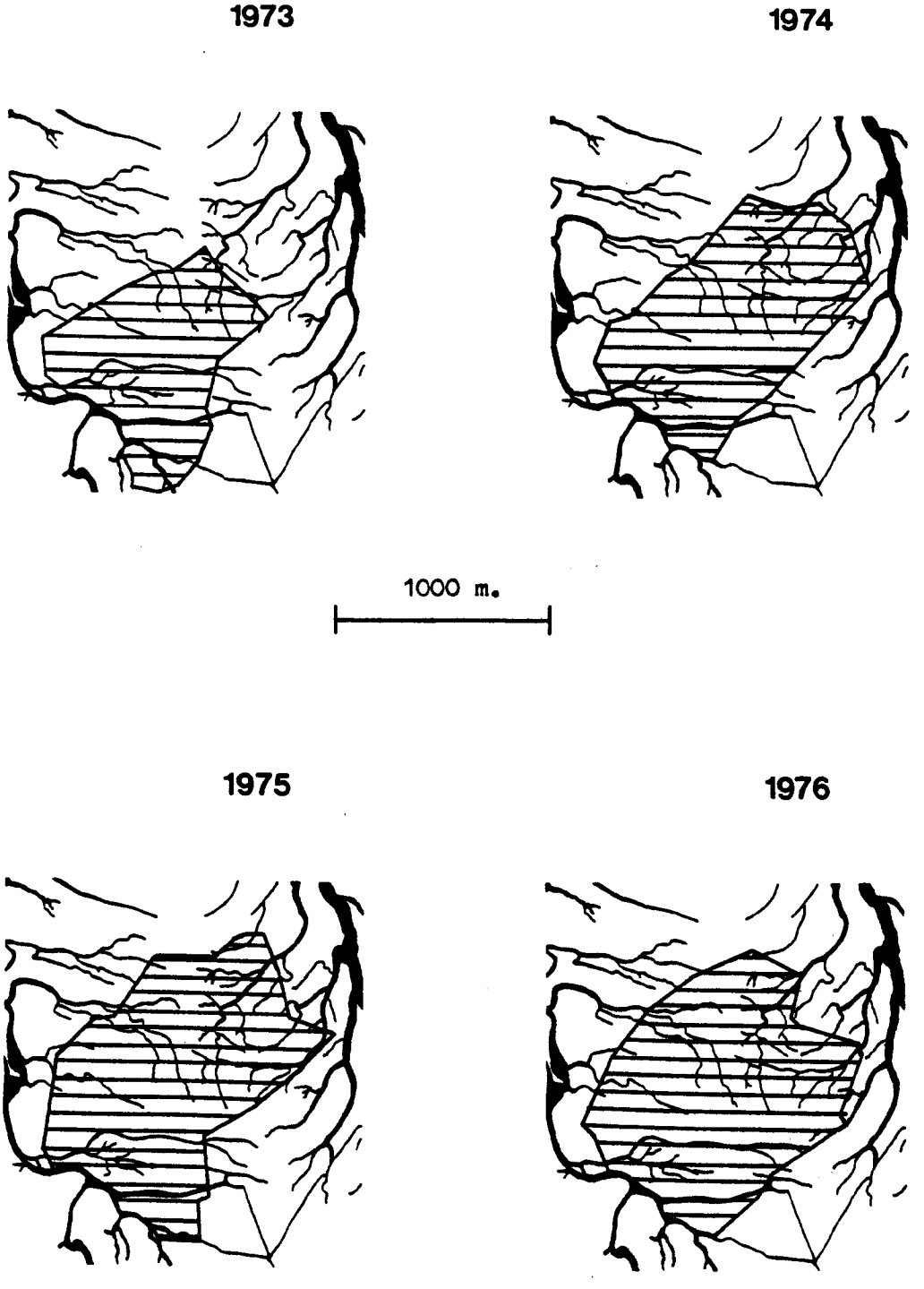


Fig. 2.2 (cont.) The Areas in Which Nests Were Found, 1973 to 1980.

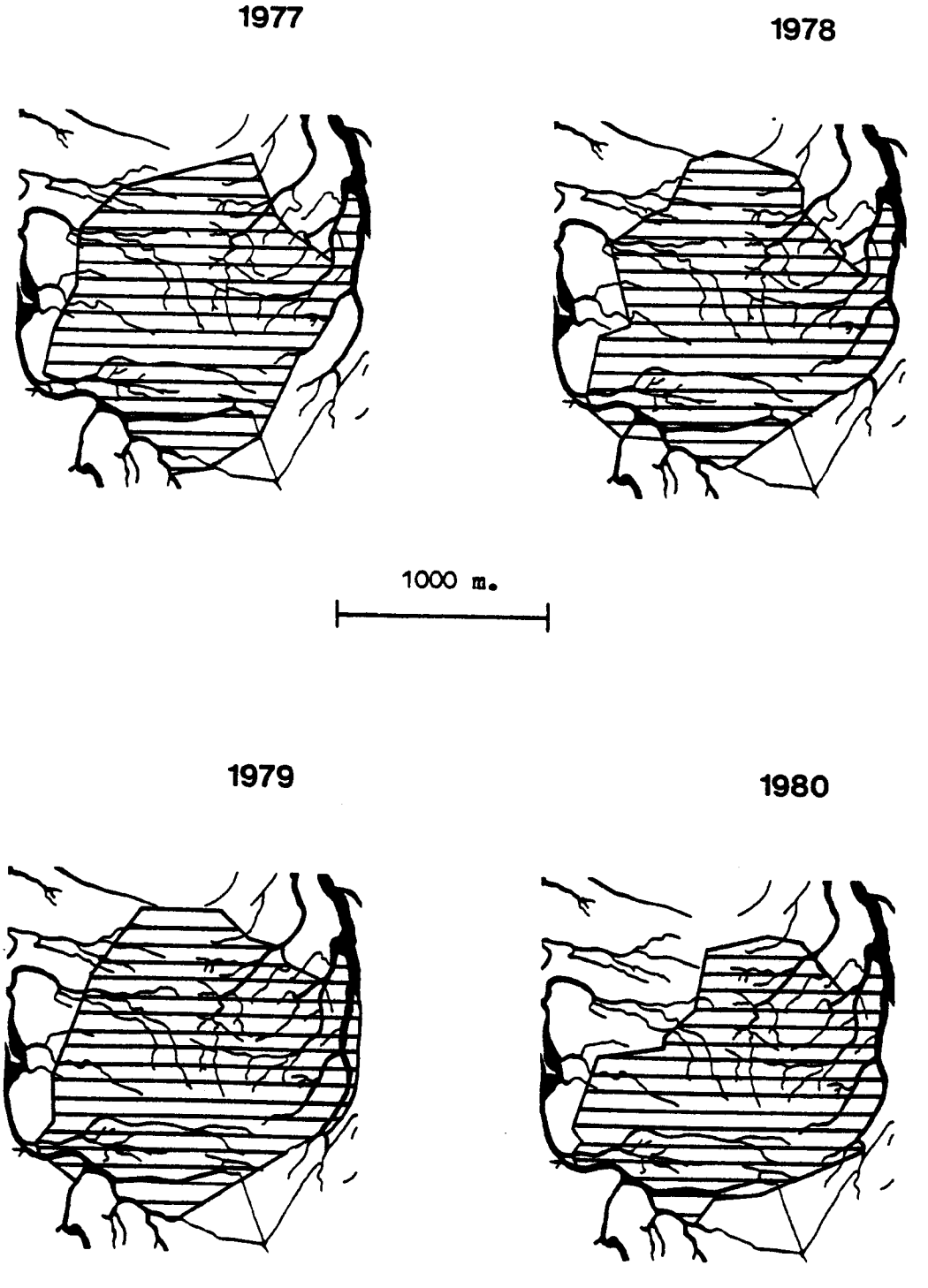


Fig. 2.3 The Restricted Area.

The polygon of the Restricted Area is shown on the map of the major channels of the saltmarsh.

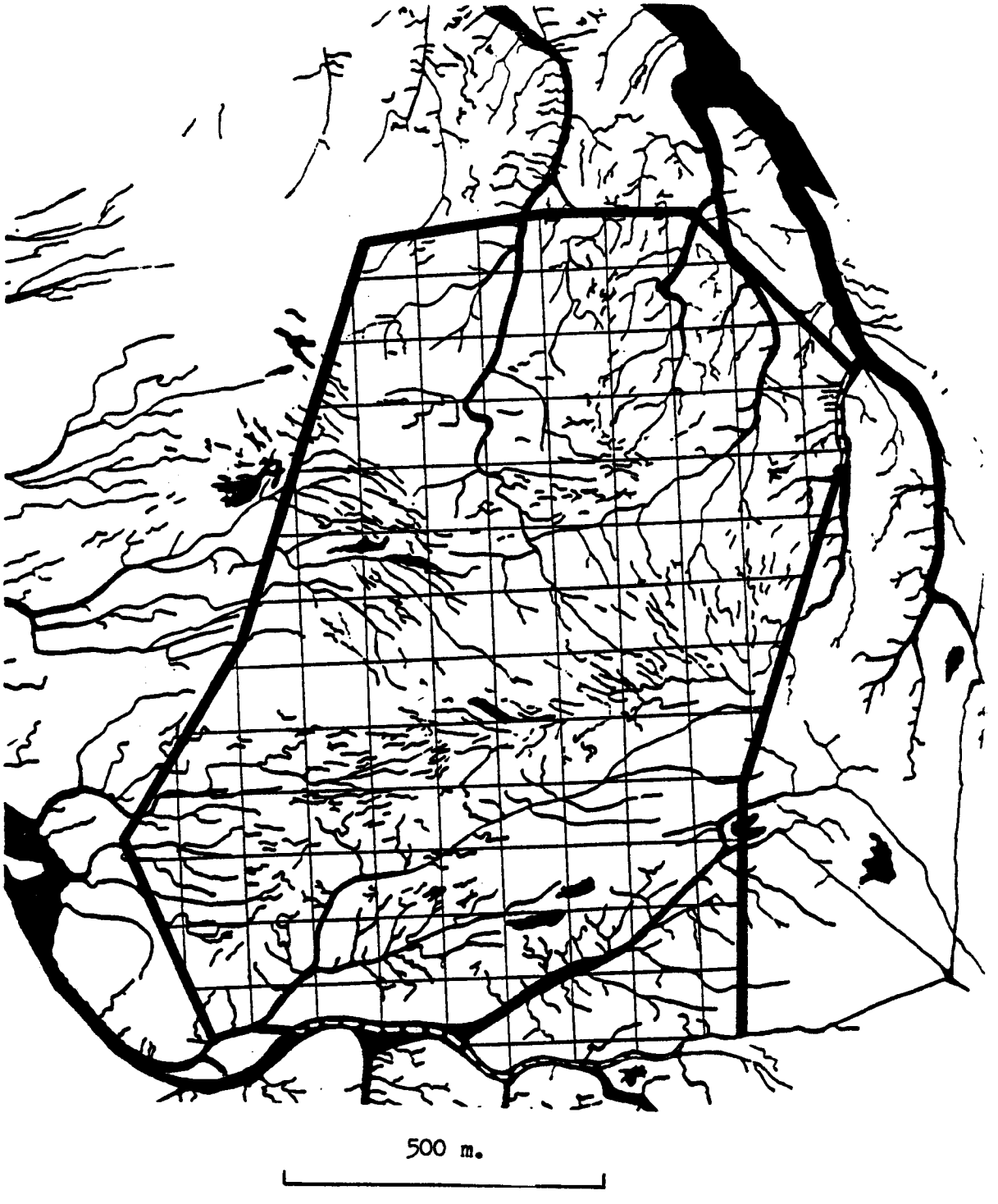


Fig. 2.4 The Vegetation Within The Study Area, With An Overlay Of Nests Found In 1981.

2.4(a) The Distribution Of Nests Found In 1981.

2.4(b) The Distribution Of The Major Vegetation Types Within The Study Area, In July 1980.

Fig. 2.4(a) The Distribution Of Nests Found In 1981.

Fig. 2.4(b) The Distribution Of The Major Vegetation Types Within The Study Area, In July 1980.

Dominant Plant Species.

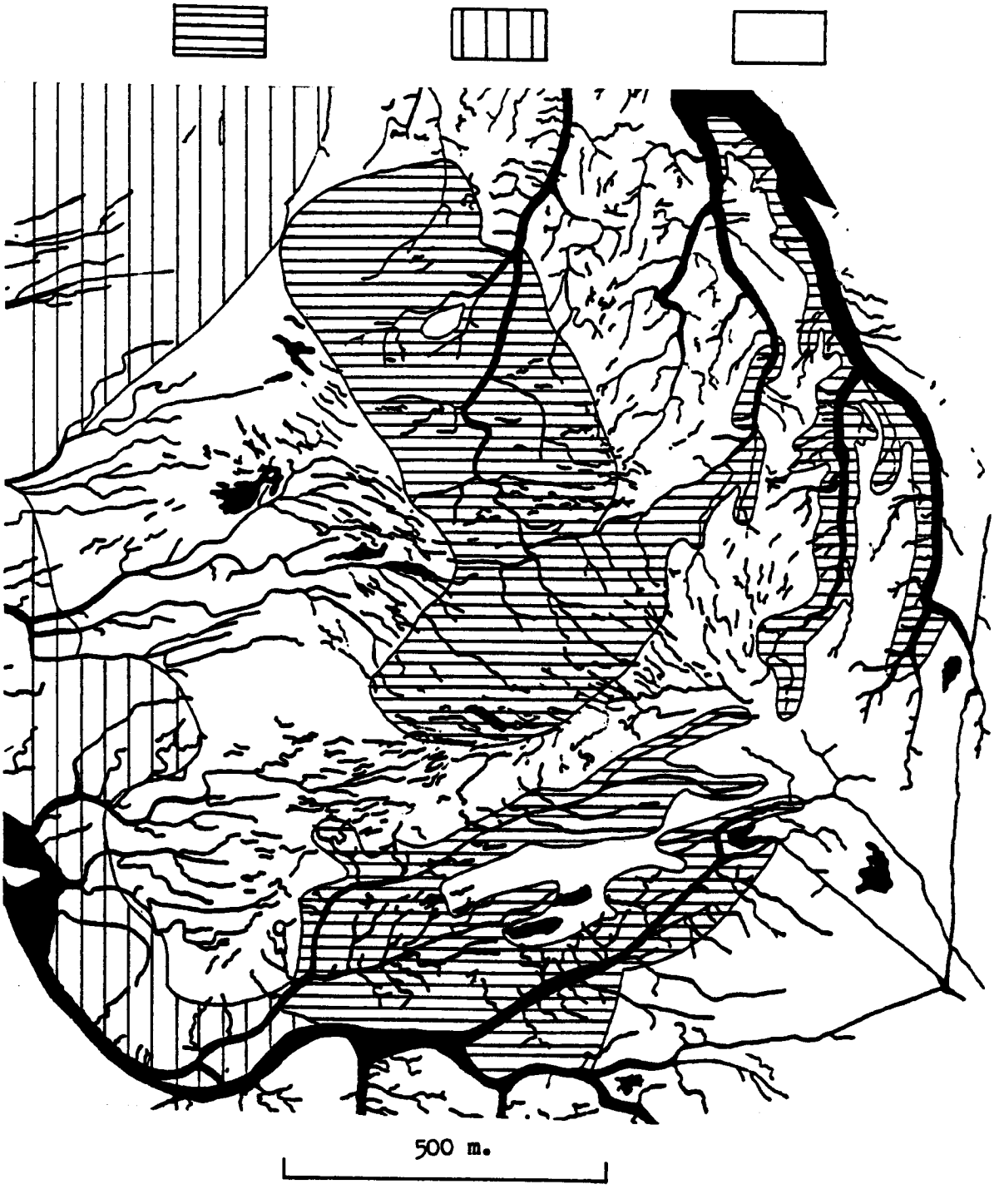


Fig. 2.4(a) The Distribution Of Nests Found In 1981.

Fig. 2.4(b) The Distribution Of The Major Vegetation Types Within The Study Area, In July 1980.

Dominant Plant Species.

Festuca rubra. Spartina anglica. Puccinellia maritima.

2.3.2 The Temporal Distribution Of Nests.

The timing of each nest cycle was taken as the date on which the last egg of the clutch was laid (also the time at which incubation began), and this was termed the date of clutch completion. For many nests this was determined exactly, by direct observation of an incomplete clutch (for example, in 1980, 42% of nests were found before clutch completion), but most were estimated from egg density measurements (see Section 4.2.1).

Only those years in which two full-time workers searched for nests , were considered, and these were from 1976 to 1981. The frequency distribution of clutch completion for the nests of these years was given in Fig. 2.5 , and represented all of the nests found on the saltmarsh, that could be accurately aged in terms of clutch completion.

Several patterns were present in these distributions, which are now discussed separately.

The six years showed differing modal frequency distributions;

1976 - a broad based unimodal distribution.

1977 - two very distinct peaks.

1978 - two very distinct peaks.

1979 - two indistinct peaks.

1980 - two very distinct peaks, with an indication of a third.

1981 - three very distinct peaks.

The atypical distribution seen in 1976 may have been due to a reduced searching effort early in the season, because of the absence of one worker, due to illness. In all subsequent years searching effort was considered comparable between years, and throughout each year. The frequency distribution of nests in 1976 will not be considered further.

Fig. 2.5 The Frequency Distribution Of The Dates Of Clutch Completion, For All Nests On The Saltmarsh, 1976 to 1981.

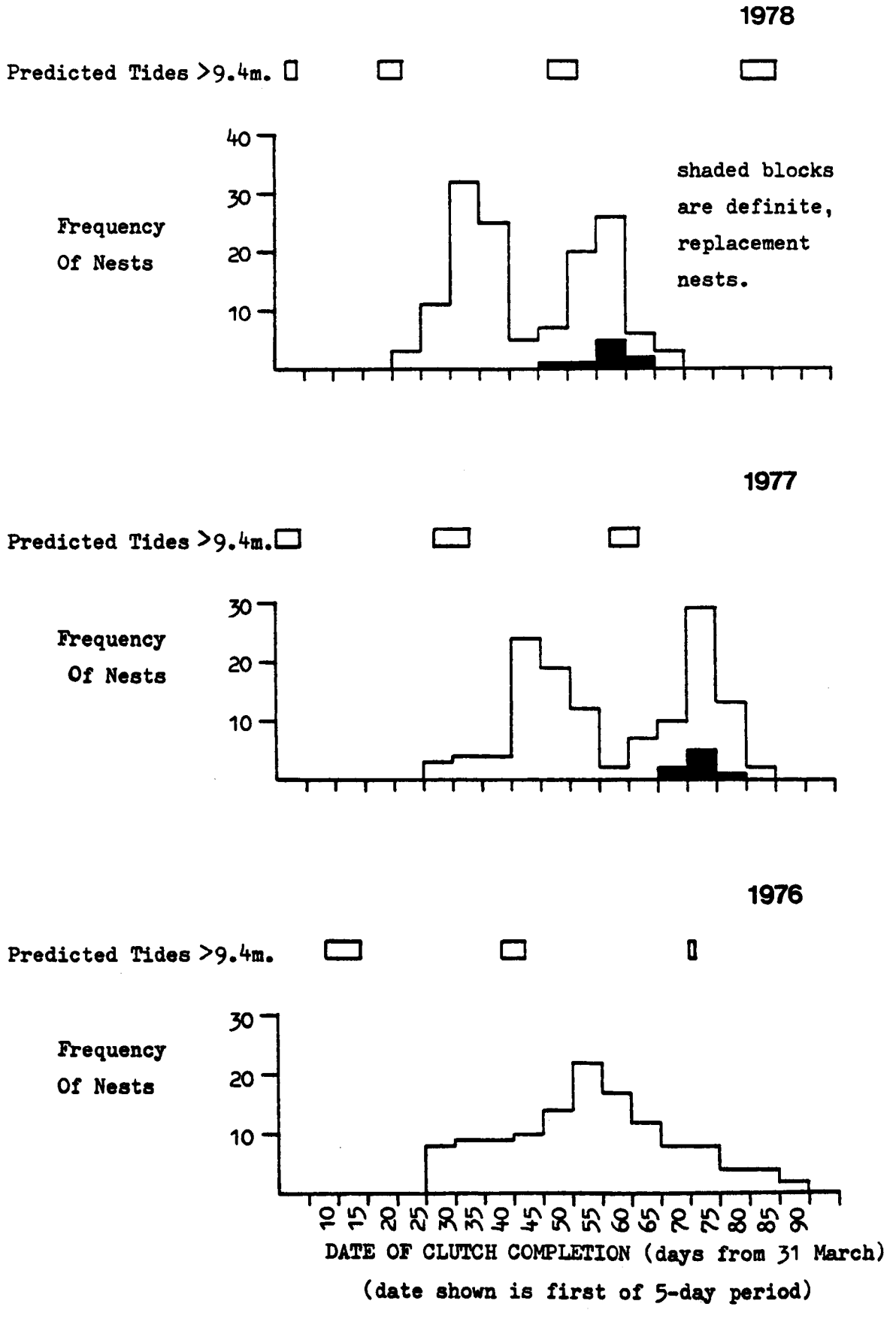
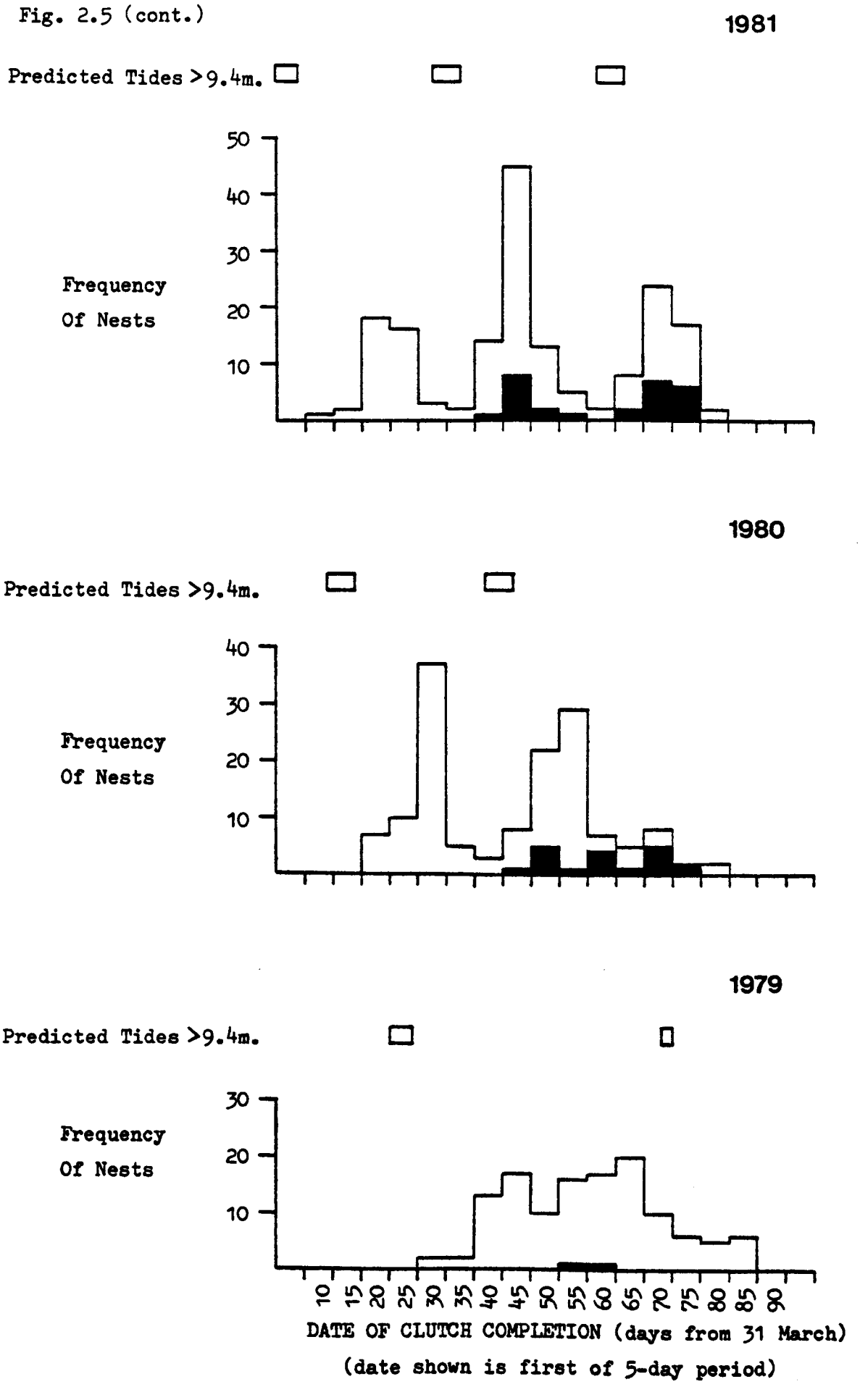


Fig. 2.5 (cont.)


1981
Predicted Tides >9.4m.
Frequency
Of Nests
50
40
30
20
10
1980
Predicted Tides >9.4m.
Frequency
Of Nests
40
30
20
10
1979
Predicted Tides >9.4m.
Frequency
Of Nests
30
20
10
10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90
DATE OF CLUTCH COMPLETION (days from 31 March)
(date shown is first of 5-day period)

The peaks of the frequency distribution of nests, were associated with the 'high spring tides' (greater than 9.4 m.) that occured, approximately, every 28 days. This relationship is considered in Table 2.1 . A peak of frequency of clutch completion occured, on average, 13.5 days after a predicted high spring tide. That is, subsequent peaks of frequency were observed approximately 25 days apart. This pattern could be spurious, such that the nests found did not faithfully reflect the nests present. The following factors may have been involved;

Firstly, following a high spring tide, the lost clutches were replaced, on average, in 13.5 days (8.9 days to lay the first egg of the replacement clutch, plus 4.6 days to complete it - see Section 4.3.7), adding to the peaks observed, on average, 13.5 days after the tide. However, for this to have been the major contribution to the following peak, many nests would have had to be lost to the tide. In 1981 this was certainly the case, but in 1980, only 6.1% of known nests were lost to the tide, and yet a large, distinct, second peak was observed.

Similarly, the decline of a peak, before a high spring tide, may have been due to nests lost to the tide, before they were discovered. Most nests were found partly incubated, such that clutch completion occured some time before their discovery. If a tide claimed many nests, the undiscovered ones were not represented in the frequency distribution, and therefore, an apparent decline would have resulted. But again, the 1980 high spring tide, following the decline of the first peak, claimed only 6.1% of known nests.

To summarise, the observed frequency distribution of the clutch completion date of nests, was distinctly multimodal in most years. The peaks of the distribution followed the high spring tides,

on average, by 13.5 days, and were approximately 25 days apart. Some of this apparently close association was due directly to nests lost to the tide before they were discovered, and to clutches, lost to the tide, being replaced. However, on the observation of only 6.1% of known nests lost to a high spring tide in 1980, with associated multimodality, doubt was cast on the above being the complete answer. There may have been a more direct link between the tidal cycle, and the timing of laying in this Redshank population. This will be discussed later.

For each year the beginning, and ending of the breeding season, were taken to be the date on which the fifth clutch, and fifth from last clutch, respectively, were completed. The duration of the breeding season was taken as the interval. These dates were considered a better assessment of the breeding season of the population, rather than the first and last clutches, because both of these would have been dependent on individual pairs, and therefore, more liable to the influence of atypical pairs.

During the six years there was a great variation in timing of the breeding seasons (see Table 2.2), and meteorological factors were considered to be a likely source of this variation.

Ashcroft (1978) observed Redshanks returning to the breeding ground during the end of March, and the beginning of April. I have, therefore, considered the period from the 1st April, until the date of completion of the 5th clutch, and obtained a mean daily figure for each meteorological parameter considered (see Section 2.2.5). Similarly, the ending of breeding occured, each year, from mid to late June, so the period considered in this case, was from 1st June, until the date of completion of the 5th from last clutch.

Table 2.1 The Timing Of The Peak Frequencies Of Clutch Completion, And The Associated High Spring Tides (> 9.4 m.).

Peak Frequencies Of Clutch Completion.	Mid-date* Of Peak (A)	Date* Of Previous Highest Tide(>9.4m.) (B)	A - B	Days From Peak-to--peak (same year)
1981 1st peak	22.5	6.5	16.0	
				25
1981 2nd peak	47.5	35.5	12.0	
				25
1981 3rd peak	72.5	64.5	8.0	
1980 1st peak	32.5	16.0	16.5	
				25
1980 2nd peak	57.5	44.5	13.0	
1979 1st peak	47.5	26.5	21.0	
				20
1979 2nd peak	67.5	-	-	
1978 1st peak	37.5	24.5	13.0	
				25
1978 2nd peak	62.5	54.0	18.5	
1977 1st peak	47.5	34.5	13.0	
				30
1977 2nd peak	77.5	64.0	13.5	
			———	—
		means	13.5	25

*Dates refered to days from 31st March, that is 1 = 1st April.

Table 2.2 A Summary Of The Timing Of The Breeding Seasons, 1976-81.

Year	Date* of 5th nest.	Date* of 5th from last nest.	Duration (days).
1976	33	87	54
1977	37	83	46
1978	31	72	41
1979	40	87	47
1980	24	74	50
1981	20	77	57

*Dates refer to the number of days from 31st March, that is, 31 = 1st May.

The duration of the nesting season is considered as the difference of the two 'date' columns.

The four independent variables (the meteorological parameters) were analysed with the dependent variable (either the date of the 5th clutch completing, or that of the 5th from last clutch), in a stepwise multiple regression. The full results are given in Table 2.3. The combined effect of the mean daily rainfall, and the mean maximum daily temperature, was to explain more than 99% of the variance of both the onset and the ending of the breeding seasons.

The mean daily rainfall was the most important single variable in determining both the onset and the ending of the breeding seasons. Fig. 2.6 showed that the beginning of breeding was delayed by high rainfall, and the ending of breeding was delayed by low rainfall. Therefore, high rainfall tended to reduce the duration of the breeding season.

Table 2.3 The Timing Of The Breeding Seasons, And The Associated Meteorological Parameters, 1976 to 1981.

Date = date of clutch completion (CC.) in days from 31st March.

Rainfall = mean daily rainfall (mm.), during the periods;
from 1st April until the date of CC. of the 5th nest, for the Onset of Breeding, or,
from 1st June until the date of CC. of the 5th from last nest, for the Ending of Breeding.

Maximum Temperature = mean daily max. temperature, for the periods indicated above, (degrees C).

Minimum Temperature = mean daily min. temperature, for the periods indicated above, (degrees C).

Wind speed = mean daily wind speed (knots.), for the periods indicated above.

Entry of variables into the regression equation was limited to those that significantly increased the determination.

The Onset Of Breeding.

Date of 5th nest = 52.49 + 5.30 Rainfall - 2.43 Max. Temperature

SE of estimate = 1.14 days

Coefficient of determination = 0.993

F = 110.81 P(2 & 3 df.) = 0.0015

The Ending Of Breeding.

Date of 5th last nest = 109.71 - 4.95 rainfall - 1.06 Max. Temperature

SE of estimate = 0.86 days

Coefficient of determination = 0.995

F = 146.00 P(2 & 3 df.) = 0.0010

Fig. 2.6 The Timing Of The Breeding Seasons, and The Rainfall, 1976 to 1981.

a) The Beginning Of The Breeding Seasons.

RAINFALL = mean daily rainfall (mm.), from 1 April until the date of CC. of the 5th nest

DATE = date of CC. of the 5th nest (days from 31 March)

$$DATE = 21.77 + 8.11\ RAINFALL$$

$$F = 66.56 \quad P = 0.0012$$

$$T_0 = 15.71 \quad P = 0.0001$$

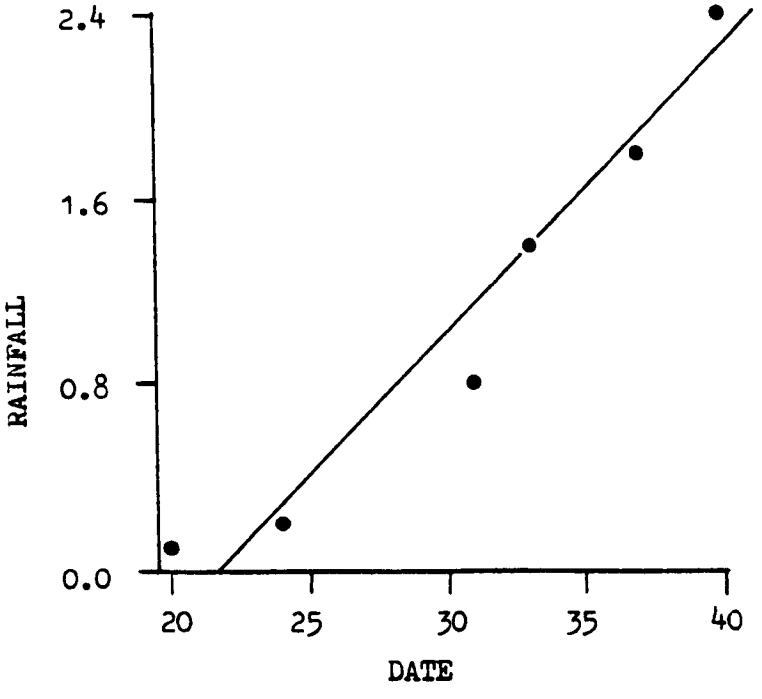


Fig. 2.6 (cont.) The Timing Of The Breeding Seasons, and The Rainfall, 1976 to 1981.

b) The Ending Of The Breeding Seasons.

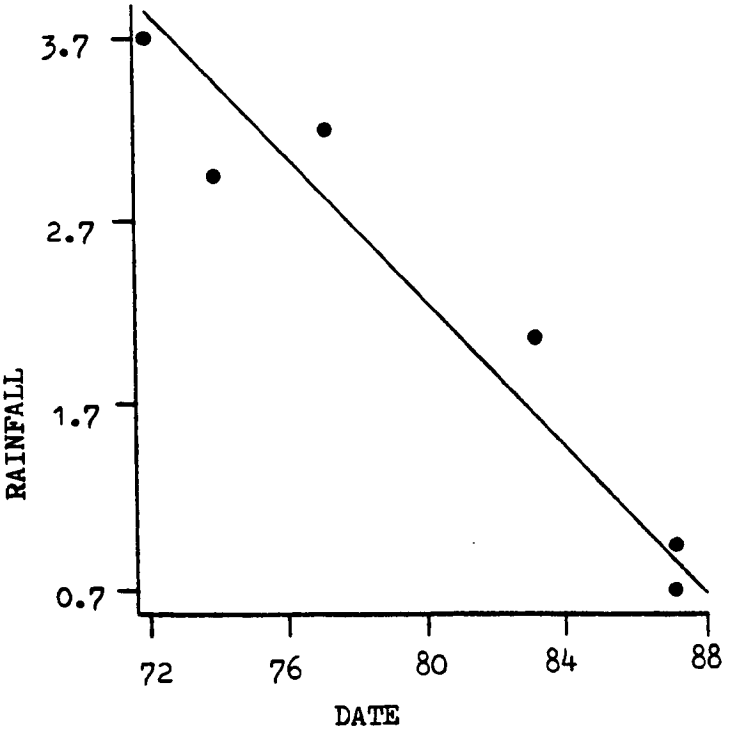
RAINFALL = mean daily rainfall (mm.), from 1 June until the date of the 5th from last nest

DATE = date of CC. of the 5th from last nest

$$DATE = 91.52 - 5.08\ RAINFALL$$

$$F = 56.50 \quad P = 0.0017$$

$$T_0 = 53.35 \quad P < 0.00001$$



2.3.3 The Spatial Distribution Of Nests.

The accurate mapping of each nest on to a detailed map of the channels on the saltmarsh, showed the overall distribution of nests (see Fig. 2.4), with many associated with the channels. However, this representation did not enable a simple analysis of the distribution. For this purpose a 100 m. grid, derived from the Ordinance Survey, was constructed within the Restricted Area. This Restricted Area Grid is shown in Fig. 2.3 . Where the boundary of the Restricted Area bisected a 100 m. square, only the area within was considered, and the density estimates were calculated thus;

In a square with only 0.2 of its area within the Restricted Area one nest would have given a density of 5 nests.ha.$^{-1}$

The grids of nests found in each year from 1974 to 1981 are given in Appendix 1 , and this is summarised in Fig. 2.7, by means of a grid of nests.ha.$^{-1}$year.$^{-1}$

The dispersion of the nests is a description of their pattern in space, and is an important aspect of the population. It can be represented by The Index Of Dispersion, which is described in Appendix 2.

Table 2.4 showed that in all years the Index Of Dispersion was significantly greater than one, and this implies a strong aggregation of nests. This may have arisen in several ways;

a) the effort expended in searching for nests may not have been even, over the entire Restricted Area, with, perhaps, concentration in some favoured search areas. This could not be ruled out, but in the last three years a conscious effort was made to spend an equal time searching in each area, and these years still showed a strong aggregation of nests.

b) different vegetation types may have been preferred for

Fig. 2.7 The Summary Of The Nest Distribution Within The Restricted Area, 1974 to1981.

Each dot represents the density of nests found, to the nearest whole nest, in units of nests.ha^{-1}.year^{-1}

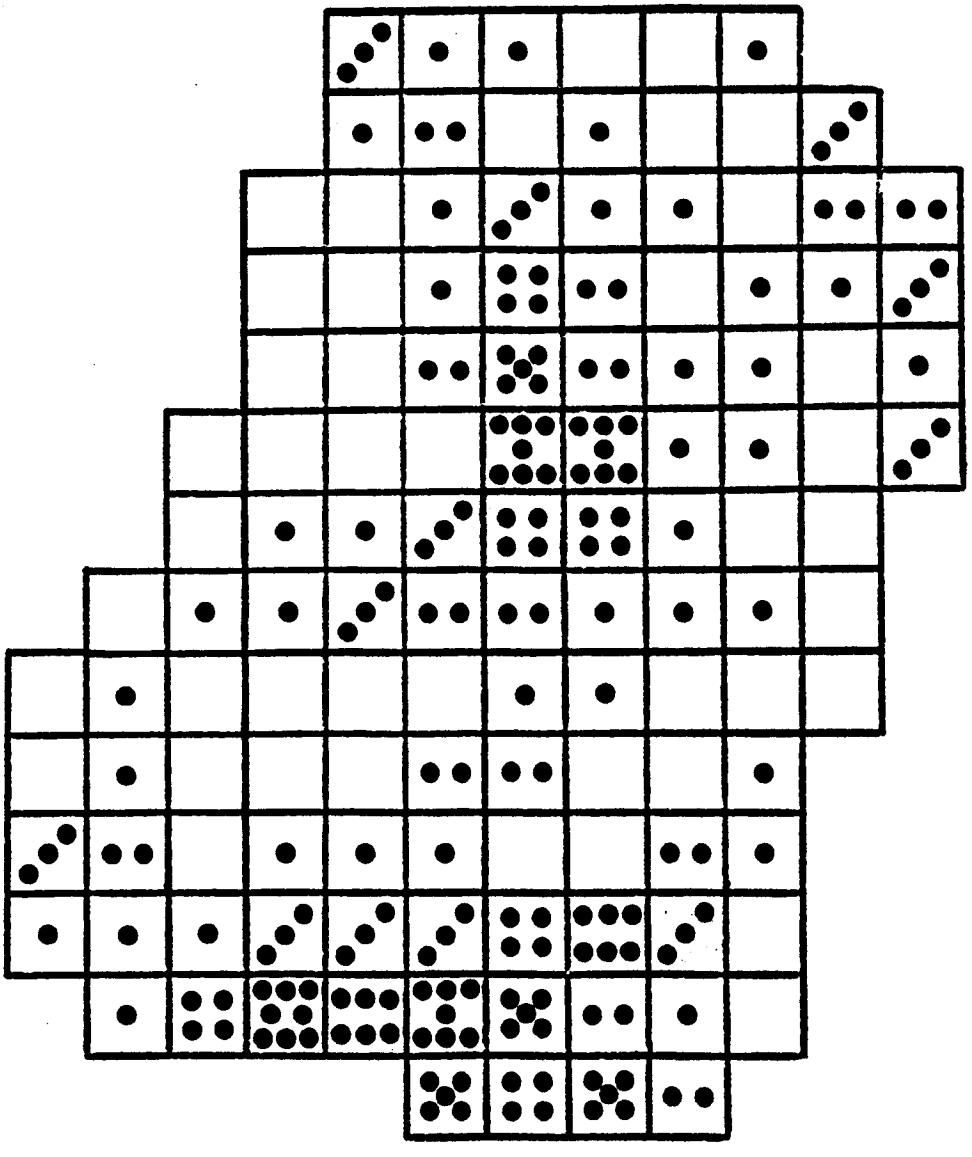


Table 2.4 The Density And Dispersion Of Nests Found Within The Restricted Area, 1974 to 1981.

Year	Variance	Mean	Chi-Square	$P(\chi^2_{N-1})$	Index of Dispersion
1974	4.01	1.33	367.83	< 0.001	3.02
1975	6.07	1.71	433.06	< 0.001	3.55
1976	5.51	1.68	400.13	< 0.001	3.28
1977	6.69	1.57	519.86	< 0.001	4.26
1978	6.91	1.50	562.01	< 0.001	4.61
1979	5.72	1.39	502.04	< 0.001	4.12
1980	2.92	1.17	304.48	< 0.001	2.50
1981	8.83	1.59	677.52	< 0.001	5.55

In all years, the Index of Dispersion was significantly greater than 1, and this implied a strong aggregation of nests.

nesting in. This is investigated later.

c) it may have been easier to find nests in certain vegetation. The preferred (see below) vegetation of tussocky, Festuca rubra provided greater cover for nests, than the other major vegetation type, Puccinellia maritima , and, therefore, may have acted against detecting the aggregation. That is, in the low density areas the nests were generally more visible, and therefore, easier to discover than in the high density areas.

d) social interaction may have facilitated the nesting of groups of birds in localised areas. With the data available, this possible factor would have been impossible to separate from the vegetation effect (see below), but it may have been important.

To be defined, in an ecological context, as a colonial species, first the individuals must be aggregated, and secondly, the aggregation must be greater than expected, based on resource patchiness (Brown and Orians, 1970). From the overlay of nests found in 1981, on the map of the vegetation of the study area (see Fig. 2.4), it was clear that the nests found were largely confined to the areas dominated by Festuca rubra. Within the Restricted Area the density of nests per hectare was correlated with the proportion of Festuca rubra in each hectare, and this is shown in Fig. 2.8 .

Therefore, until a detailed assessment of the resource patchiness is undertaken, that evaluates the habitat in terms of the Redshank's requirements for a nest site, it cannot be termed a colonial species.

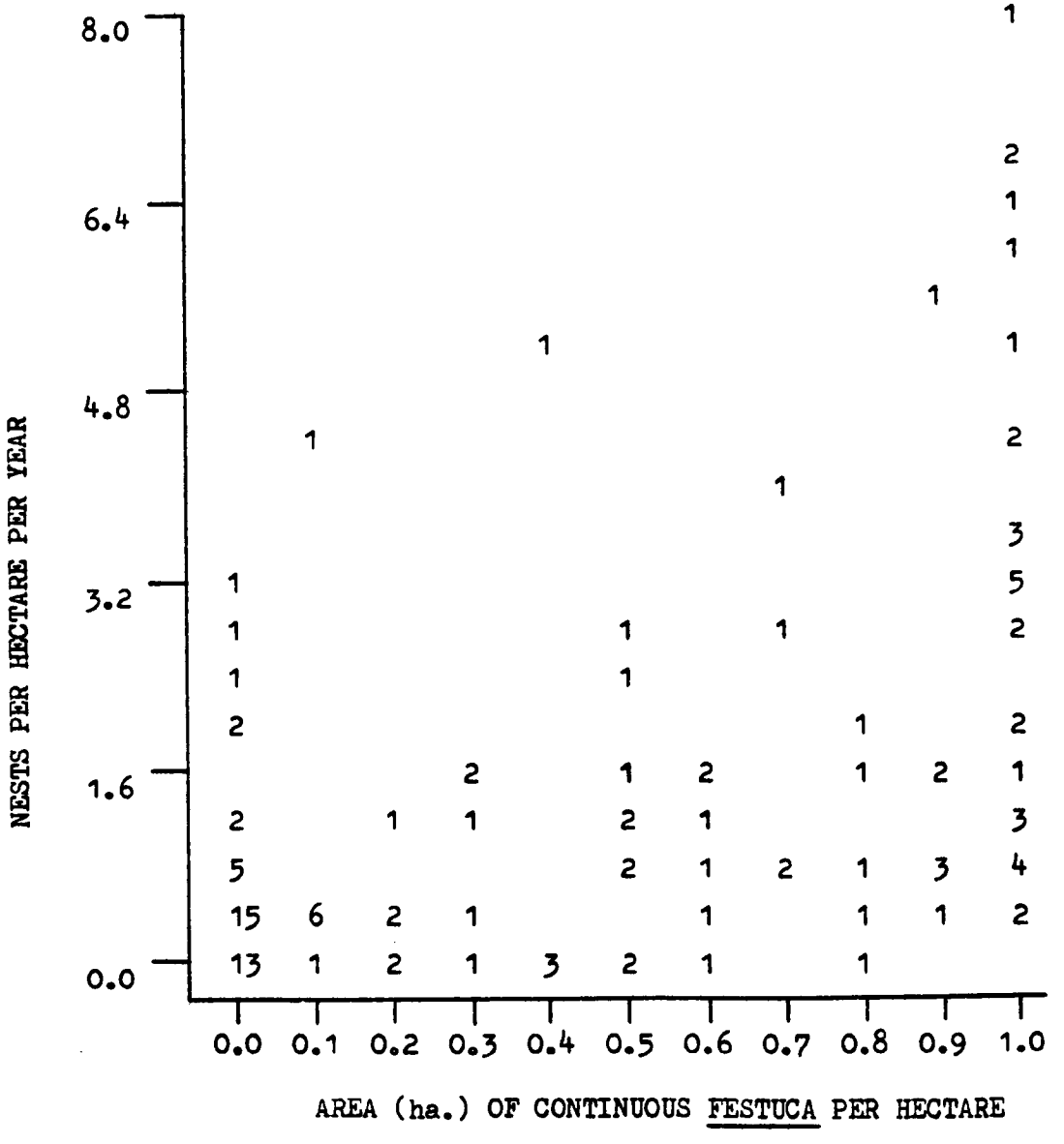
Fig. 2.8 The Relationship Of The Nest Density and The Distribution Of Festuca rubra.

Spearman rank-order correlation analysis;

$r_s = 0.562$

$N = 123$

$P < 0.001$



2.3.4 Nest Losses.

The data in Table 2.5 shows the fate of all nests found on the saltmarsh, and represented a very coarse summary, which was useless in estimating nest losses.

Serious errors result from determining nest losses by dividing the number of nests observed, into the number that failed to to hatch (Mayfield 1961 and 1975, and Johnson 1979). This follows from the undetected number of nest losses in the sample of nests, found after the beginning of incubation. The result of this error is to underestimate nest losses.

In this study approximately 60% of nests were found after the beginning of incubation, and so the method of Mayfield (1975) was used, together with the standard error of Johnson (1979). Details of this method is given in Appendix 3.

Nest Losses By Predation.

The analysis by the method of Mayfield (1975) of the nest losses by predation is shown in Table 2.6. There was no significant difference between the losses in the fenced and unfenced areas in 1979, and so the total for 1979 was taken for comparison with the other two years. Nest losses by predation in 1979 were significantly higher than in both 1980 and 1981, but there was no significant difference between the latter two years.

It was considered that the vegetation may have influenced the predation rates, and so an annual comparison was made with the general height of the vegetation on 1st April, see Fig. 2.9. With only three points for comparison a rank correlation could not be applied, but the ranking of both parameters was in absolute agreement.

Table 2.5 The Fate Of All Nests Found On The Saltmarsh, 1979 to 1981.

Year	1979	1980	1981
Total saltmarsh nests.	172	160	197
Total nests of known fate.	148	150	184
Hatched	50 (33.8%)	78 (52.0%)	69 (37.5%)
Predation loss	17 (11.5%)	1 (0.7%)	3 (1.6%)
Flooded	9 (6.1%)	11 (7.3%)	44 (23.9%)
Trapping loss	14 (9.5%)	40 (26.7%)	44 (23.9%)
Deserted	6 (4.1%)	5 (3.3%)	6 (3.3%)
Crushed	23 (15.5%)	0	3 (1.6%)
Addled	1 (0.7%)	9 (6.0%)	2 (1.1%)
Uncompleted	28 (18.9%)	6 (4.0%)	13 (7.1%)
Old	24	10	11

The percentages, in brackets, refer to the 'Total nests of known fate'.

This table represents a crude analysis of the fate of all nests found on the saltmarsh.

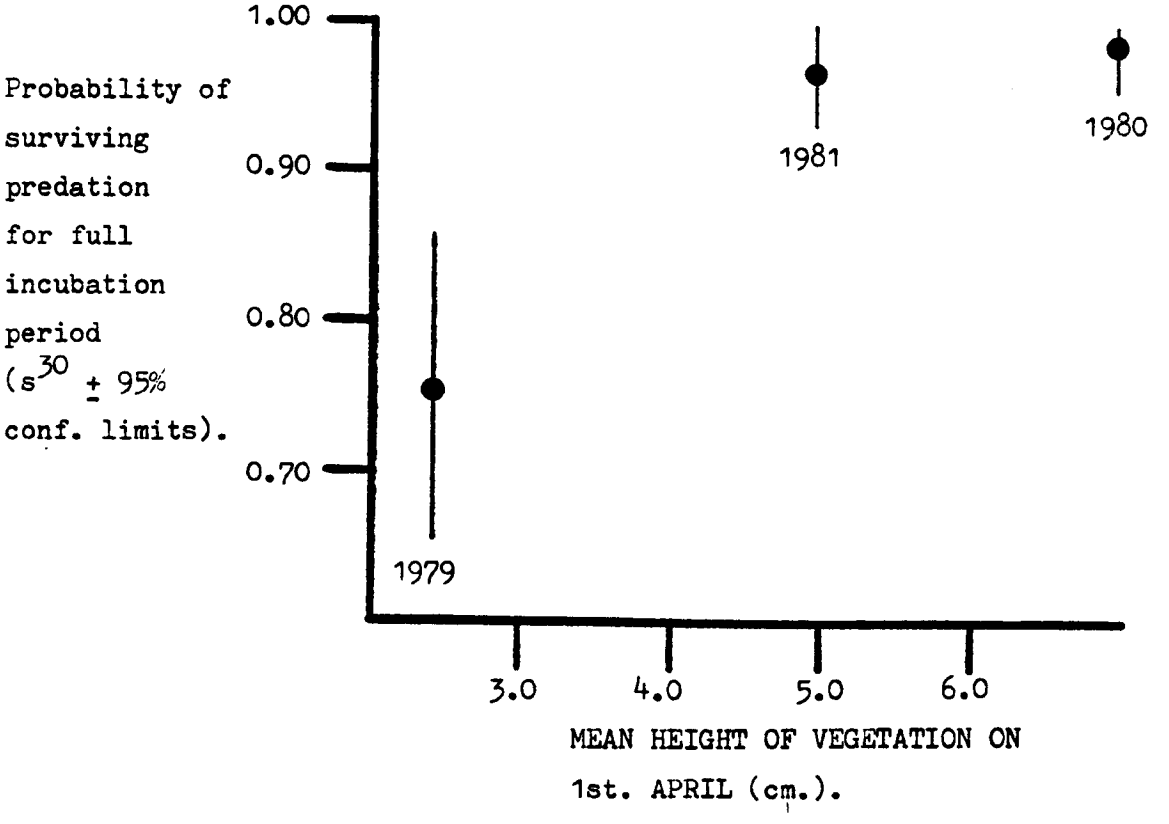
Table 2.6 The Mayfield Analysis Of Nest Losses Due To Predation, Cattle And Natural Desertion.

	PREDATION LOSSES					CRUSHED	NATURAL DESERTION			
* Sample.	1979 F.	1979 U.	1979 T.	1980 T.	1981 T.	1979 U.	1979 T.	1980 T.	1981 T.	All Years.
Exposure (days).	657	1151	1808	2125	2885	1151	1808	2125	2885	6818
Losses.	6	11	17	1	3	23	6	5	6	17
Nest mortality, m.	0.0091	0.0096	0.0094	0.0005	0.0010	0.0200	0.0033	0.0023	0.0021	0.0025
Nest survival, s.	0.9909	0.9904	0.9906	0.9995	0.9990	0.9800	0.9967	0.9976	0.9979	0.9975
$S.E._s$	0.0037	0.0029	0.0023	0.0005	0.0006	0.0041	0.0014	0.0011	0.0008	0.0006
95% range of s^{30}.	0.850 to 0.679	0.892 to 0.630	0.864 to 0.656	1.014 to 0.959	1.005 to 0.935	0.702 to 0.424	0.982 to 0.834	0.991 to 0.873	0.988 to 0.892	0.962 to 0.895
s^{30}.	0.759	0.750	0.753	0.986	0.969	0.546	0.905	0.932	0.940	0.928

s^{30} is the probability of a nest surviving the full nesting period of 30 days.

* the "sample letter codes" are as follows; T = total, F = fenced area, U = unfenced area.

Fig. 2.9 The Relationship Of Nest Predation And Vegetation Height.



This tentatively indicated a dependence of the predation rate upon the height of the vegetation.

In 1979, however, there were sufficient nest losses by predation for further analysis of this problem. The cover estimates for the total nests, were compared with those lost by predation by chi-square analysis in Table 2.7 (see also Fig. 2.10).

The cover index of nests lost by predation was significantly lower than that of other nests, and this was due to significantly more "0-1 cover", and significantly fewer "7-8 cover" nests in the predation loss catagory.

Nest Losses Due To The Cattle.

For the analysis in Table 2.6 , only the nests of the "1979 unfenced area" were used, because it was only these that had a continuous grazing pressure.

As above, the cover estimates of crushed nests was compared with those of other nests, by chi-square analysis in Table 2.7 (see also Fig. 2.10). There was no significant difference between the cover of nests crushed by cattle and that of all other nests.

Overall the cattle accounted for approximately 45% of all nests deserted , a very great impact on the population, that was removed in the last two years of the study by fencing, to exclude all cattle.

Nest Losses By The Tides.

The tide periodically covered all, or part of the study area, and during the breeding season could result in the loss of

Fig.2.10 The Nest Cover Estimates Of The Nests in 1979, Grouped According To Fate.

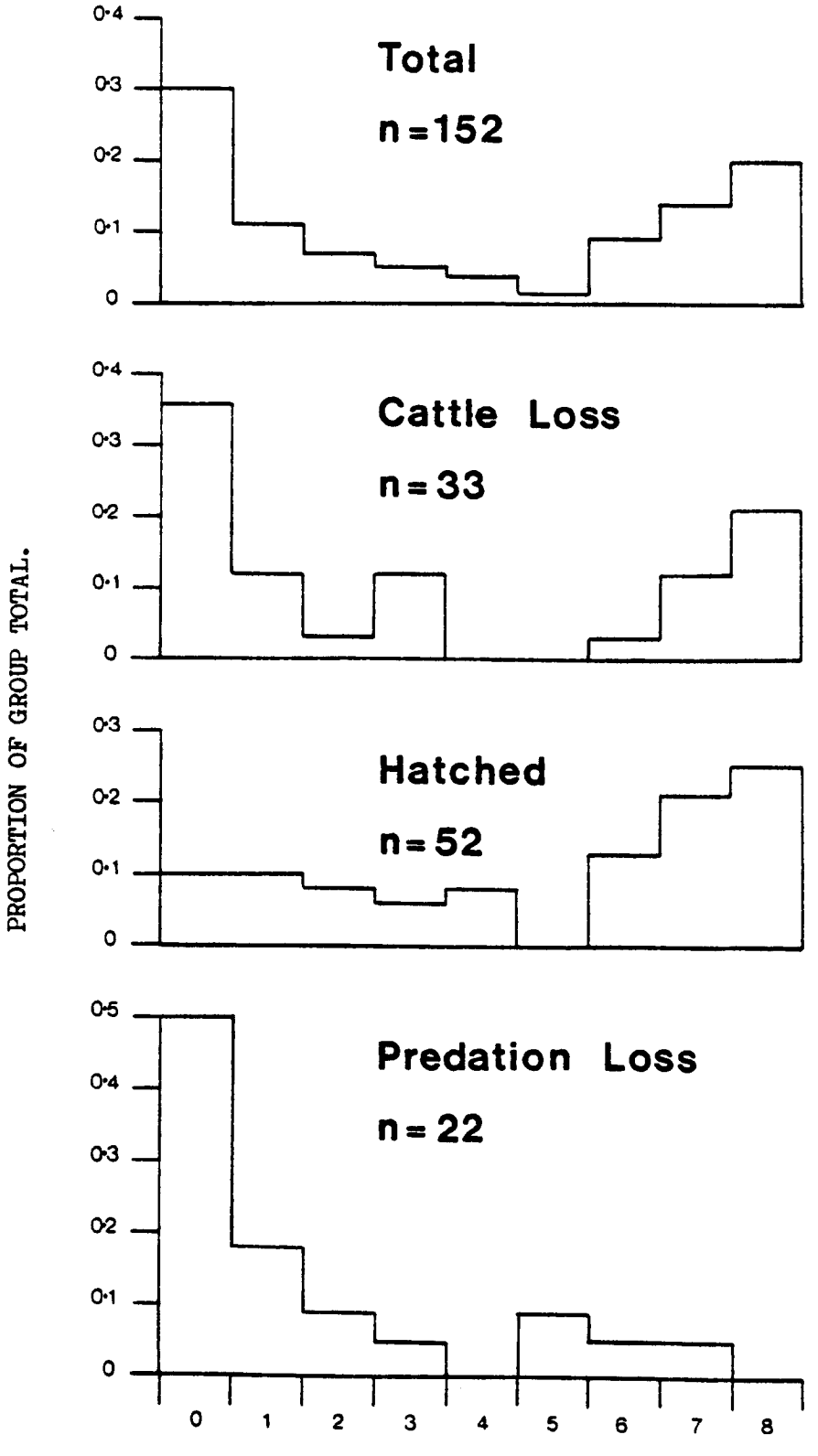


Table 2.7 The Analysis Of The Estimated Cover Of Nests, In Relation To Their Outcome, In 1979.

Fig. 2.10 shows the frequency distribution of the cover estimates for the 3 catagories of outcome; a) lost due to predation
b) lost due to cattle
c) hatched

These are compared below with all other nests.

a) Nests Lost Due To Predation.

Cover estimate	Predation	Others	Total	χ^2	P
0-1	15	46	61	4.82	< 0.05
2-6	6	34	40	0.00	n.s.
7-8	1	50	51	6.55	< 0.025
Total	22	130	152	11.37	< 0.005

b) Nests Lost Due To Cattle.

Cover estimate	Crushed	Others	Total	χ^2	P
0-1	16	45	61	0.74	n.s.
2-6	6	34	40	1.06	n.s.
7-8	11	40	51	0.00	n.s.
Total	33	119	152	1.79	n.s.

c) Hatched Nests.

Cover estimate	Hatched	Others	Total	χ^2	P
0-1	10	51	61	8.61	< 0.005
2-6	18	22	40	2.07	n.s.
7-8	24	27	51	5.81	< 0.025
Total	52	100	152	16.49	< 0.001

clutches. Some clutches could survive complete submersion, if they were newly laid (that is, they did not float), and the nest had enough protective vegetation surrounding it, to hold the eggs against the water current. However, many clutches were lost each season, but, because the risk was only sporadic, this loss was not investigated by the method of Mayfield (1975).

The analysis assessed the proportion of the total known nests that was lost to the tide, and compared this to the tide height.

Two estimates of the tide height were used. First, was the predicted height of the tide for Liverpool, 33 km. to the south. This predicted tide was subject to variation due to a complex of meteorological factors. Secondly, the observed tide height within the area of Preston Port, 12 km. to the north-east. This latter measurement should have been a closer estimate of the tidal activity on the study site.

Table 2.8 showed the available data on the tides and nest losses, and the significant positive correlation between the percentage of known nests lost, and the actual tide observed at Preston.

Nest Losses By Trapping.

During 1981 a detailed record was kept of the trapping activities, and this is summarised in Table 2.9 .

The total number of birds caught was 252, and these took an average of 2.4 trapping attempts each to capture. The figure of greatest importance was the 26.5% of nests, at which trapping was attempted, that deserted, because of the trapping. This was higher than what might have been considered an acceptable level, but it only

Table 2.8 The Tide Heights And Associated Nest Losses, 1979 to 1981.

Approximate Date.	Percentage Of Known Nests lost.	Predicted Liverpool Tide (m.)	Observed Preston Tide (m.)
15-5-79	7.7	9.3	no record
14-6-79	5.9	9.5	8.53
12-7-79	37.5	9.8	8.75
15-5-80	6.1	9.7	8.58
15-6-80	14.6	9.4	8.78
15-5-81	69.4	10.0	9.00
4-6-81	30.2	9.7	8.78

Spearman Rank Order Correlation Analysis.

Predicted Liverpool Tide.

$$r_s = 0.670$$

$$P(5 \text{ df.}) > 0.1$$

Observed Preston Tide.

$$r_s = 0.814$$

$$P(4 \text{ df.}) < 0.05$$

Despite the limited data, this table showed the significant positive correlation between the observed tide height, and the observed proportion of known nests that were lost to that tide.

Table 2.9 The Summary Of Adult Trapping In 1981.

Number of birds caught from each nest.	2	1	0	Total
Total number of nests.	102	48	16	166
Total number of trapping attempts.	360	200	40	600
Mean number of trapping attempts per nest.	3.5	4.2	3.0	3.6
Number of nest losses due to trapping.	18	21	5	44
Percentage of nests that deserted, following trapping.	17.6	43.8	31.3	26.5

The total number of birds caught was 252, and these took an average 2.4 trapping attempts each to capture.

affected about half of the total population of nests of the study area. In addition, many of the nests that deserted, were replaced. Therefore, trapping probably resulted in breeding failure for less than 10% of the total population.

Nest Losses By Natural Desertion.

The analysis of these losses by the method of Mayfield (1975) in Fig. 2.6 , showed no significant difference between years, so the total value was considered as the best estimate. Overall, only 7% of nests failed because of natural desertion.

The Success Of Surviving Nests.

The nests that survived the full period of incubation did not necessarily produce a pullus from every egg, as shown in Table 2.10.

The mean number of pulli produced per successful nest was only 2.53 . Some of the failure was due to partial loss of the clutch during incubation, but the major cause was eggs failing to hatch.

Table 2.10 The Number Of Pulli Hatching In Successful Nests.

Year	1981	1980	1979	Total
Pulli hatched per nest.				
0	2	8	5	15
1	10	19	6	35
2	15	18	7	40
3	22	23	22	67
4	18	15	16	49
Total number of nests.	67	83	56	206
Total number of pulli.	188	184	150	522
Mean number of pulli per nest.	2.81	2.22	2.68	2.53

2.3.5 Replacement Nests.

A nest found early in the season was almost certainly a genuine first nest, but later, there was a greater chance that it was a replacement nest, following the loss of a nest (or brood). Replacement nests were considered to be the second (or occasionally third) nest of the season, for a pair, or member of a pair. The positive identification of replacement nests was only possible when the same adult(s) was caught off both nests, and so many (possibly most) were not detected.

The estimated periods from the end of incubation at one nest, and the laying of the first egg in the replacement, were shown for the years from 1977 to 1981, in Table 2.11 . The very long periods probably resulted from intermediates being missed, while the very short periods probably resulted from the desertion of a nest by only one member of the pair (see Section 3.3.6).

There was no significant difference between the periods of the sexes, with most (53%) laying the first egg 4-9 days after the end of incubation of the previous nest.

The outcome of the first nest did significantly affect the period. First nests that hatched were replaced after a longer period than those that failed to hatch. Assuming that the first brood had perished, this increase in time possibly represented the period in which the brood was surviving (the increase in the median period was 3 days).

The number of males recorded from replacement nests was more than twice that of females, and the following may have accounted for most of this difference. There was a 24% divorce rate within years

Table 2.11 The Interval Between Nests Of Individuals Within A Year.

The interval used is from the ending of activity at the first nest, to the laying of the first egg in the replacement clutch, for the years 1977 to 1981.

Interval (days)	Males	Females	Total
0	1	0	1
1-3	5	3	8
4-6	14	6	20
7-9	13	7	20
10-12	7	4	11
13-15	4	0	4
16-18	4	1	5
19-21	1	1	2
22	3	1	5
Total	52	23	75

Most nests (53%) were replaced after 4-9 days.

The influence of nest success on the interval.

First nests that hatched are compared to those that failed to hatch, by chi-square analysis.

	Interval (days)		
	≤ 9	> 9	Total
Hatched nests	5	12	17
Failed nests	44	14	58
Total	49	26	75

$\chi^2 = 13.87 \quad P < 0.001$

Therefore, nests that hatched, and were replaced, took longer to be replaced (median, 10 days) than the nests that failed to hatch (median, 7 days).

(see Section 3.3.6), and the females with new mates were more likely to move out of the study area (see Section 3.3.5). In addition, there was probably a greater strain on the females in producing a replacement clutch, and a proportion may not have done so.

The timing of the known replacement clutches was shown in Fig. 2.5 , and in the next section it is assumed that all nests failing during the "first peak", and none of those in the "second peak", were replaced. This was a necessary over-simplification of a very complex aspect of the breeding biology, that could not be investigated further, with the available information.

2.3.6 The Overall Nest Loss And Pulli Production.

Details in this chapter have described the variation in nest loss , due to varying environmental influences, so a single estimate of production would be of little value.

The differing environmental influences measured during this study, can be combined in several ways, to determine the possible range of production in the population. In this way the impact of the separate causes of nest loss can be more easily observed.

When estimating the pulli production, a major consideration was the frequency of replacement of failed nests. The details in this chapter enabled the following general assumption to be made; all failed nests in the first nesting peak, and none in the second, were replaced.

Three general cases of environmental conditions were considered;

Case 1 - largely based on 1979. Two peaks of nesting, with each enduring a tide claiming an average proportion of nests (0.25). Summer grazing by cattle followed winter grazing by sheep.

Case 2 - similar to above, but no winter grazing by sheep, and therefore predation was lower.

Case 3 - again, similar to above, but no summer grazing by cattle.

The results are shown in Table 2.12 . Under the assumptions of this model the production of pulli varied up to three fold, from 0.73 to 2.28 pulli.pair^{-1}. There was a general difference between pairs nesting in the first and second peaks, because of the assumptions, but the major impact on the population was clearly the cattle.

Table 2.12 The Overall Nest Loss And Pulli Production.

Environmental conditions (see text)	1	2	3
P(surviving nesting period) = s^{30}, for different nest losses.			
Predation loss	0.75	0.98	0.98
Losses due to cattle	0.55	0.55	1.00
Losses due to tide *1	0.75	0.75	0.75
Natural desertion	0.93	0.93	0.93
Overall s^{30}	0.29	0.38	0.68
Nest survival in two peak frequencies of clutch completion. *2			
First Peak; First nests (s^{30})	0.29	0.38	0.68
Second Peak; First nests (s^{30})	0.29	0.38	0.68
Replacement nests ($(1-s^{30})s^{30}$)	0.21	0.24	0.22
Pulli Production, *3 (pulli.pair^{-1}).			
First peak pairs (including replacement nests)	1.27	1.57	2.28
Second peak pairs (no replacement nests)	0.73	0.96	1.72

ASSUMPTIONS.

*1 - an average tide resulting in 25% nest losses.

*2 - all first peak nests, and no second peak nests were replaced.

*3 - tha average of 2.53 pulli per successful nest was used.

2.4 Discussion.

Timing of laying.

The timing of the breeding seasons studied was correlated with the mean daily rainfall, and to a lesser extent with the mean maximum daily temperature, whereas the aspect considered most important by Grosskopf (1959b) was the mean daily temperature. A major consideration of this effect is the influence of the weather on feeding, which is presumably important during the period of egg formation. Perrins (1970) stated that for birds generally;

"Laying cannot begin until food has become sufficiently abundant for each female to find enough food (in addition to that needed for general body maintainence) without risk to itself."

In the Red-billed Quelea Quelea quelea the proximate control of breeding is provided by the individuals own body condition, particularly the state of its protein reserves (Jones and Ward 1976).

The winter feeding of several wader species has been studied with respect to the meteorological conditions (for example, Goss-Custard et al 1977 and Dugan et al 1981), but there is no work directly relevant to the Redshank during the breeding season. Rainfall reduces the rate of feeding of the Redshank's preferred food, Corophium spp., and hence its availability to the birds (Goss-Custard 1970), so this may be a controlling factor. In the Swift Apus apus rainfall (plus low temperature and strong wind) delayed laying in the population and it was clear that this resulted from the reduction in aerial insect abundance (O'Connor 1979).

Another consideration is the inhibition of courtship behaviour by adverse weather conditions. Heavy rainfall and extremely low temperatures were suggested by Ashcroft (1978, p.29)

to inhibit the display flights of the males, which would delay pair formation and, consequently, egg laying.

In contrast to the present study, however, Holmes (1966) reported that the Dunlin Calidris alpina in N. America began laying at the same time each year despite fluctuations in the weather. Similarly, in the same species in N. Europe, Soikkeli (1967) determined little variation in the timing of the beginning of the breeding season.

No other wader species studied in detail has shown a consistent multimodal frequency distribution of the timing of nesting, as was found in the Redshank in this study. A factor considered as the possible cause of this pattern was a mechanism, with strong selective force, to reduce the risk of nest losses to the high spring tides. The interval between these periods of high risk is 28 days, which is too short to produce and incubate a clutch, and rear the pulli past the critical age of about four days (see Section 5.4); this requires approximately 35 days. If a clutch is layed just before a series of high spring tides it would have to endure two periods of high risk. By timing the beginning of laying just after these periods a clutch would endure only one period of high risk.

Nest losses.

Another mechanism that probably resulted in fewer nest losses to the tides was the observed preference for nesting in Festuca rubra. This vegetation dominates the drier, and therefore higher, areas (especially the raised banks of the channels), which were the last to be affected by the tides.

The very low predation rate of nests that was observed in most years followed from the large amount of cover at the preferred

nest sites. This prevented an increase of predation at high nest densities, as shown for open ground nests by Gorranson et al (1975). A similar pattern was reported for the Turnstone Arenaria interpres , but in this case the observed greater losses of the open nests was due to intraspecific predation (Vuolanto 1968).

The activity, and therefore success, of potential nest predators, such as Herring Gull Larus argentatus , Lesser Black-backed Gull L. fuscus and Carrion Crow Corvus corone , over the study area was probably reduced by the antipredator behaviour of the large, diffuse colony of Common Tern Sterna hirundo.

The massive nest losses due to the presence of the cattle on the saltmarsh constitute a factor that could easily be controlled; this would increase nesting success by 46%. By removing this cattle pressure from the study area in the last two years (and from a proportion in other years, see Section 2.2.4) it enabled the population to compensate for some of the nest losses caused by my own disturbance. The latter could only be assessed in terms of the percentage of pairs that deserted after trapping at their nests (that is, 26%). The effect on the total population was much less than this because not all nests were found and trapped each year, and clutches deserted early in the season could be replaced.

In waders the proportion of eggs that fail to hatch varies greatly, both within a species (between habitats), and between species; for example, Heppleston (1972) investigated the Oystercatcher Haematopus ostralegus and found a range of failure from 0.08 to 0.53, while Boyd(1962) reveiwed many species and found ranges from 0.04 to 0.44 . Two estimates have been made for the Redshank; 0.14 by Grosskopf (1958, 1959) and 0.04 by Nordberg (1950). This study

generated several estimates of nest loss, dependent upon the environmental conditions prevailing. By combining these losses with the mean number of eggs hatching per nest, it was possible to produce the range of 0.20 to 0.45 for the proportion of eggs laid that failed to hatch.

The dispersion of nests of waders within the habitat varies considerably. Highly territorial species, such as the Golden Plover Pluvialis apricaria , show a regular distribution (Ratcliffe 1976), whereas a few, such as the Upland Sandpiper Bartramia longicauda , are considered to nest colonially (Bowen 1975). In the present study the Redshank showed an aggregated distribution in all years. This distribution cannot yet be termed colonial since the nest density was correlated with the distribution of Festuca rubra , which itself was localised.

CHAPTER THREE - THE ADULTS.

3.1 Introduction.

The measurements made on breeding adults are assessed for their usefulness in the estimation of an adults' size and sex. A regime for estimating sex is developed as a necessity for further investigations.

From the detailed histories of individuals' mates and nest sites, it is possible to examine two types of fidelity. These are faithfulness to a previous nest site, and to a previous mate. In addition, the interaction of these two is investigated.

The major section of this chapter considers the annual survival and the population size of the breeding adults, using the method of capture-recapture analysis. This analysis is dependent on the investigations outlined above for the interpretation of the results, and in testing the assumptions of the mathematical model used.

The influence of adult age and mate faithfulness on the date of laying within a season is investigated to determine if it could be these factors that give a selective advantage to the high degree of mate fidelity.

Finally, the reports of individuals outside the breeding season enable the factors influencing the distribution of a single breeding population to be considered.

3.2 METHODS

3.2.1 Trapping the Adults.

Following the discovery of a nest, and the taking of the measurements previously described, it was important to catch the pair of adults. The following trapping regime was developed, to balance the needs for data collection, with causing the minimum of disturbance.

I attempted to trap adults only at nests which were estimated to have been incubated for at least four days. The traps were of the 'walk - in' type, made of wire mesh, with a single funnel entrance and standing about 50 cm. tall and 50 cm. diameter. They were set by being placed over a suitable nest, with the funnel entrance positioned over the birds' pathway to the nest. They were then secured to the ground, with wire stakes, and left for an incubating bird to return. Each trapping period was limited to a maximum of three hours. Following a capture, a 'rest period' of one day was given to the nest.

Exceptions to this did occur, when a nest was near hatching, or in danger from a high tide.

The trapping did represent a large amount of disturbance, and resulted in some desertions. The rest period did complicate the trapping, but was essential for capturing as many individuals of the population as possible, and providing the maximum information on each bird.

The trapping period of three hours was, I consider, near the limits that could be employed. It resulted from the large area of the study site, and the large number of traps to be set each day (up to 35). However, it also resulted in the cooling of the eggs, when an adult did not return, or the occasional capture of two adults

at one time.

Observations of some returning birds showed a great variation in behaviour. Some entered without hesitation, while a few were so wary that they would not enter. Most fell between these extremes, and after a few minutes would enter and settle on the clutch.

Approaching a trapped bird usually caused it to leave the nest, and walk to the far end of the trap. Here it was taken out and placed in a cotton bag. However, some would jump and flap about, whilst others could be taken off the nest (a very few individuals were caught like this without using a trap).

It was at this time (or if previously disturbed in the trap), that some damage could be done to the bird. Most frequently this was at the base of the bill, and the carpal joint of the wing, usually causing only minor abrasion.

Very occasionally (only 3 times in 9 years), three different birds were caught from one nest. This resulted from a single bird being caught, and then two others together. This may be explained as follows; of the two together, only one was from the nest, entering the trap first and attracting another (not its mate) in. Evidence for this came from the behaviour of some birds seen when approaching a trapped bird. Occasionally a small flock of Redshanks formed around the trapped bird. It was not too difficult from this to infer that one of these could also have become accidently trapped, resulting in a 'false pair'.

To be further considered is the hypothetical occasion, when such a false pair is trapped, and the real member of the nest pair escapes from the trap. These false pairings would not have been detected, since trapping at a nest ceased when two different birds

had been caught from it.

This was an unknown factor that I considered to have occured at a very low frequency, but it must not be forgotten.

3.2.2 Processing the Adults.

Following capture at a nest, an adult was either fitted with an individually numbered ring, or, if already ringed, identified by its ring number. In all years from 1973 to 1981, the following measurements were made, to estimate the size of each bird;

a) Weight - this was determined to 1.0 g. using a '300 g. Pesola spring balance'. The bird was placed in a cotton bag of known weight for weighing.

b) Wing length - the distance between the carpal joint, and the tip of the longest primary feather was determined to 0.5 mm., with a stopped rule, using the "flattened, straightened wing" method of Spencer (1976), with the exception of opening the wing for measurement.

c) Tail length - the distance between the 'root', and the tail tip, was determined to 0.5 mm. The side of one point of a pair of dividers was placed against the body, and the other at the tip of the longest feather; the distance was measured against a rule.

d) Bill length - the distance from the bill tip to the feathering, on the dorsal side, was determined, using dividers as above, to 0.5 mm.

e) Tarsus length - the length of the tarso-metatarsal was determined to 0.5 mm., using dividers to measure the distance from the depression in the angle of the intertarsal joint, to the base of the last complete scale before the toes diverged.

f) Tarsus width - the width of the tarso-metatarsal bone

at the mid-point, was determined to 0.01 mm. using a vernier caliper, with a pressure clutch, that ensured comparable estimates of this soft measurement.

In addition, an estimate of the amount of breeding plumage attained was made. The number of breeding feathers in a two and a half centimetre square of the breast and mantle was counted (see Hale 1971).

For the last two years a measurement of the width of the cloacal opening was made to 0.5 mm., by placing a rule across it. This was initiated to aid the determination of sex.

In the last season a final measurement was taken, in an attempt to find a distinct difference between the sexes. This was the 'Skull length', the distance from the back of the skull to the tip of the bill. It was measured with a stopped rule to 0.5 mm.

When considering sex differences the comparison of the members of a pair was known to be a comparison of one male and one female. A further comparison of a group of males with a group of females was made possible by the formation of 'Pairing Complexes'. These were produced as follows;

if bird A paired with bird B at one nest, bird C with bird D at another, and bird B with bird D on another, the pairing complex below, was produced;

one sex	other sex
A	B
D	C

After several years study many such groups were produced (with a maximum of thirty-two individuals in each), and these proved

very useful in the comparison of the sexes.

3.2.3 Colour Marking the Adults.

All the adults captured in the years 1973 to 1979 were fitted with a unique combination of coloured, plastic leg rings, in addition to the numbered, metal rings. This was to enable individuals to be identified without recapture, and promote reports of birds away from the breeding area. The method used, however, had certain drawbacks;

a) positioned below the intertarsal joint, the rings were very difficult to see in vegetation, and were liable to be covered with mud in intertidal areas.

b) the rings were subject to great wear from repeated exposure to saltwater, mud and sunlight, resulting in several colours becoming indistinct, and causing confusion of the individual colour combination.

c) the occasional loss of rings also confused the combinations.

These problems resulted in very few observations of value being made from the colour rings.

In 1980, therefore, patagial wing tags were fitted to a sample of birds in an attempt to follow their broods in the study area. These tags were very similar to those described by Anderson (1963), but were smaller, measuring only 16 mm. x 39 mm. Each was one of three colours and marked with one of thirty-one distinct characters, each 17 mm. tall.

These proved more successful than the colour rings, allowing some observations of parental behaviour to be made, and provided many reports away from the breeding area.

3.3 RESULTS.

3.3.1 The Variation Of Adult Measurements.

The measurements taken from each adult captured were intended to estimate, objectively, its size. However, each measurement taken throughout the study contained various errors that resulted in a deviation from the real size of each bird. These errors could have resulted from differences between observers, years, times of season, stages of incubation, times of day and/or tidal cycle. The total effect of these was investigated by a one way analysis of variance of the measurements of birds caught in five years (these were chosen to maximise replicates of both years and birds). The full analyses are given in Appendix 4 , and are summarised in Table 3.1.

For all measurements, except tail length,the variation was significantly greater between birds than within (that is, repeated measurements of individuals). The tail length showed an extremely large amount (97.9%) of the total variation, within birds, and therefore, individual measurements of tail were not used further in this study.

The great variations of tail length within an individual probably resulted from differences in feather wear, combined with the difficulty experienced in determining the precise position of the base of the tail.

Weight also showed a large variation within birds (43.7%), and this was considered in Fig. 3.1 where weights of individuals caught more than once within a nesting cycle were plotted against the time from the beginning of incubation. No overall trend was determined, but it was clear that some individuals could lose more than 10g. within a very few days. Some large increases were also observed.

Variation of cloaca width could not be analysed so intensively

Table 3.1 A Summary Of The Analysis Of Variance Of Adult Measurements.

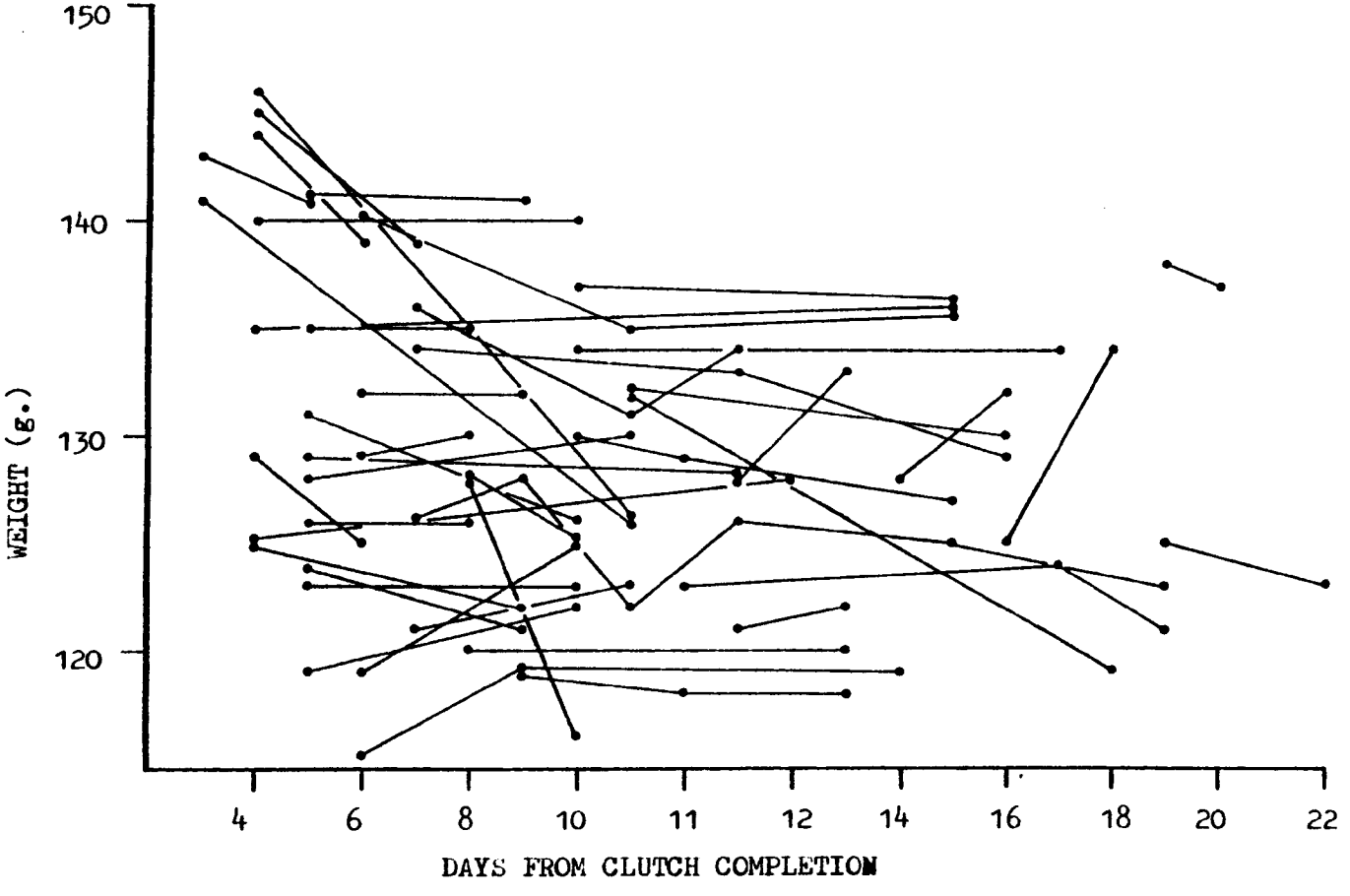
A one way analysis of variance of the measurements of all birds caught in five years was computed. The full results are given in Appendix 4, and a summary is given below.

Measurement	Mean	Standard Error	Probability (F-test)	Percent of Variation Within Birds **1
Weight (g.)	132.13	2.78	< 0.001	43.7
Wing (mm.)	167.65	0.68	< 0.001	22.2
Bill (mm.)	41.89	0.44	< 0.001	24.6
Tarsus len.(mm.)	48.74	0.52	< 0.001	27.6
Tarsus wid.(mm.)	2.412	0.028	< 0.001	37.0
Tail (mm.)	65.83	2.44	> 0.1	97.9

For all measurements, except tail length, the variation was significantly greater between birds than within (that is, repeated measurement of individuals).

**1 - this is also termed the coefficient of interclass correlation - see Sokal and Rohlf, 1969, p.211.

Fig. 3.1 The Recorded Changes In Body Weight Of Adults Within One Nesting Cycle.



because this measure was only made in the last two years of the study. However, Fig. 3.2 showed a very few repeat measurements within a nesting cycle, and no overall trend of change was determined, and in Fig. 3.3 the measurements of individual birds between years were consistent, with a significant positive correlation.

3.3.2 The Sexing Of Breeding Adults.

Without an accurate sexing procedure of the birds trapped, very few investigations could have been carried out, but the sex of an individual bird posed one of the greatest difficulties of this study. The plumage and size of the sexes were so similar that there was no means of separating them in the hand.

Previous studies of the Redshank have used the slight size differences of the sexes as a means of differentiating them. Hale (1971) used sexed museum specimens to show this slight sexual dimorphism.

Grosskopf (1958) classed the member of a pair that was distinctly heavier and with a longer wing, as the female. He stated that, "this classification of sex was supported later by the observations of behaviour, faithfulness to their territory, and behaviour on change of partners. There were no contraditions.". His study used size to determine sex, and then characterised the sexes in terms of size - a circular argument (although backed up by some observations) that would tend to exaggerate any sexual dimorphism.

In contrast to Grosskopf (1958) the present study showed many contradictions to the rule that the largest member of a pair was the female (see Table 3.3). Further, there were many cases in which both members of a pair were very similar, such that the variation

Fig. 3.2 The Recorded Changes In Cloaca Width Of Adults Within One Nesting Cycle.

Points joined by a line refer to one bird.

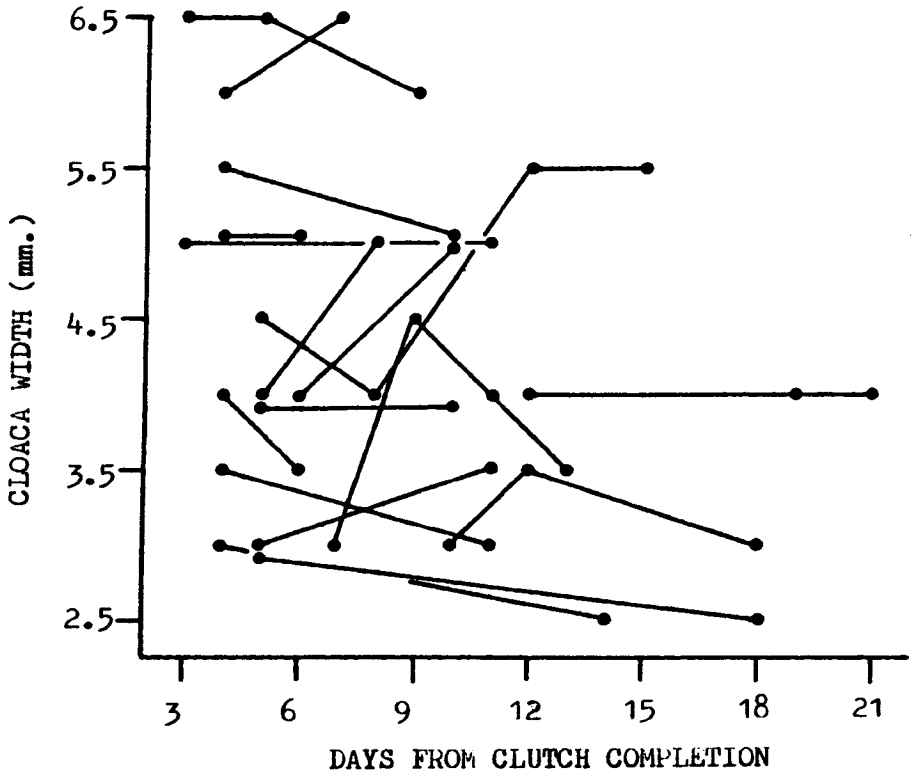
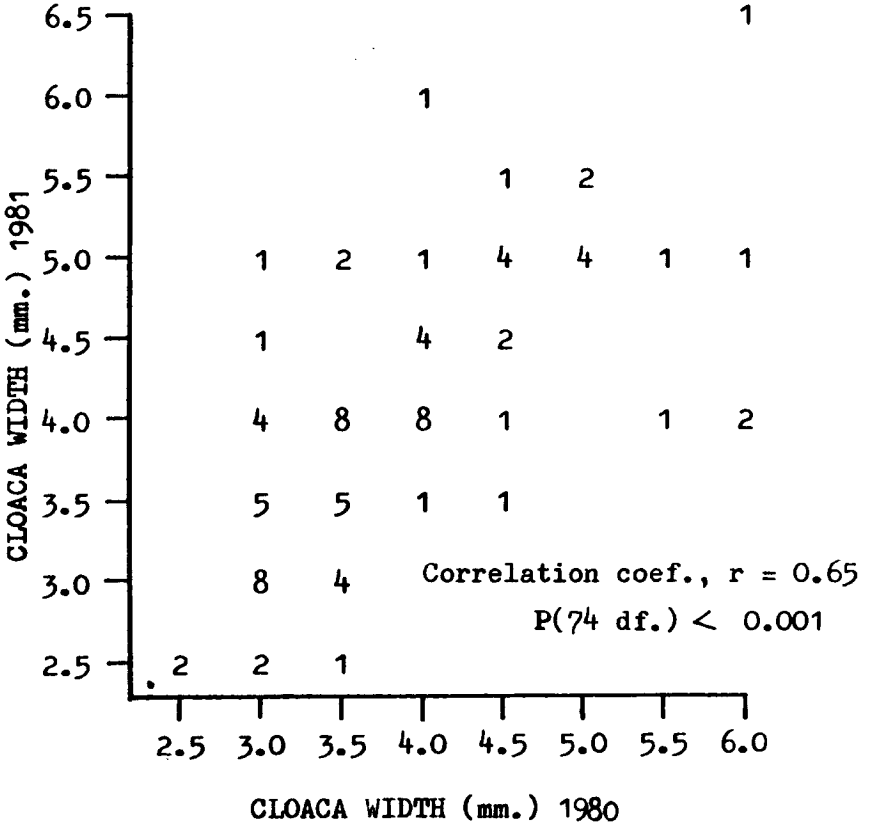


Fig. 3.3 The Recorded Changes In Cloaca Width Of Adults Between Years.

The figures indicate the number of birds at each point.



of measurement described previously could have affected the sex determination.

It was, however, possible to investigate the size characteristics of the sexes by utilising the constancy of the mean egg volume of a clutch (M.E.V.) for a particular female. A full investigation of egg size parameters in different clutches of the same female is given in Section 4.3.1 , which demonstrates that the M.E.V. is the most consistent size parameter between clutches of the same female.

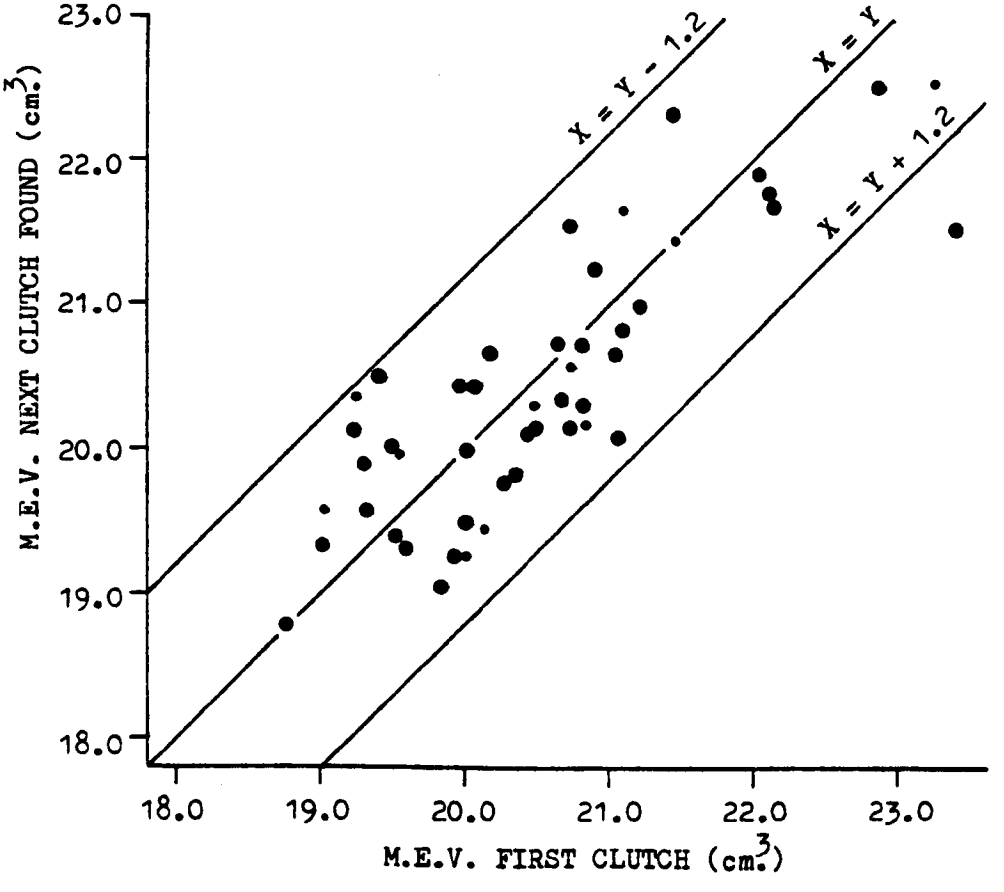
The M.E.V. produced by a particular PAIR was compared with that of the next clutch found of the SAME PAIR. This ensured that the two M.E.V.'s applied to the SAME FEMALE. The data involved 37 between year, and 11 within year comparisons (see Fig. 3.4). The first clutch (X) was plotted against the next clutch found (Y), and a line of $X = Y$ was found to be a good fit. Further lines of $X = Y + 1.2cm.^2$ and $X = Y - 1.2cm.^2$ enclosed 47 (97.9%) of all points.

From this it was determined that if the M.E.V.'s of two clutches differed by more than $1.2cm.^2$ they were probably produced by different females. This depended on the assumptions that the male of a pair contributed nothing to the M.E.V. of a female - this could be false if courtship feeding occurs in the Redshank, or if 'good' males took their mates to better feeding areas, but these have never been recorded.

All clutches not definitely known to have been produced by the same pair, but with a common individual, were compared. Where a difference of M.E.V. greater than $1.2cm.^2$ was found, the bird common to both clutches was classed as MALE. By this method many males would

Fig. 3.4 The Distribution Of The Mean Egg Volume (M.E.V.) For Successive Clutches Of The Same Female.

$X = Y + 1.2cm.^3$ encloses 97.9% of all observations.



Large dots represent between year comparisons.

Small dots represent within year comparisons.

have been overlooked, simply because many females would, by chance, lay clutches of similar M.E.V.

Only 29 individuals were classed as male by this 'M.E.V. method', but this was increased to 64 by using the 'pairing complexes' (see Section 3.2.2). These males were paired with 85 females.

These two groups were not selected on the basis of their size, or plumage characteristics, so they were used for further investigations to determine a method for sexing all adults. This 'M.E.V. method' of sexing breeding Redshank was seen to be valid from the results of Section 4.3.4 (Table 4.6), where the egg size is significantly positively correlated with female size, but not with male size.

Frequency distribution histograms for the two sexes, of the measurements at last capture, of weight, wing length, bill length, tarsus length and width, cloaca width and skull length are given in Fig. 3.5 . The parameters of weight and wing length showed a slight separation of the sexes, but the best distinction was of cloaca width, which is summarised in Table 3.2 .

The consideration of the measurements of breeding pairs (sexed by the M.E.V. method only) permited a very simple comparison in Table 3.3, which determined the largest of a pair. The greatest separation of the sexes was clearly by weight (despite the large potential fluctuations of this measurement - see Table 3.1), in which the female was the largest in 72% of pairs. The mean weight of males at last capture was 127.2g., and for females it was 134.8g. The mid-point of these two was 130.9g.

With this information it was possible to draw up the

following regime to estimate the sex of all breeding adults caught.

Sexing Members Of A 'Pairing Complex' Or Single Pairs.

If individuals were sexed as male by the 'M.E.V. method', then the group (within the 'pairing complex' - see Section 3.2.2) was sexed as male. If not the two groups were compared in terms of their cloaca widths, and the group that showed the larger values was considered female. With no available cloaca measurements (or only a few), then the weights were considered, and the group with the heavier individuals was taken as female.

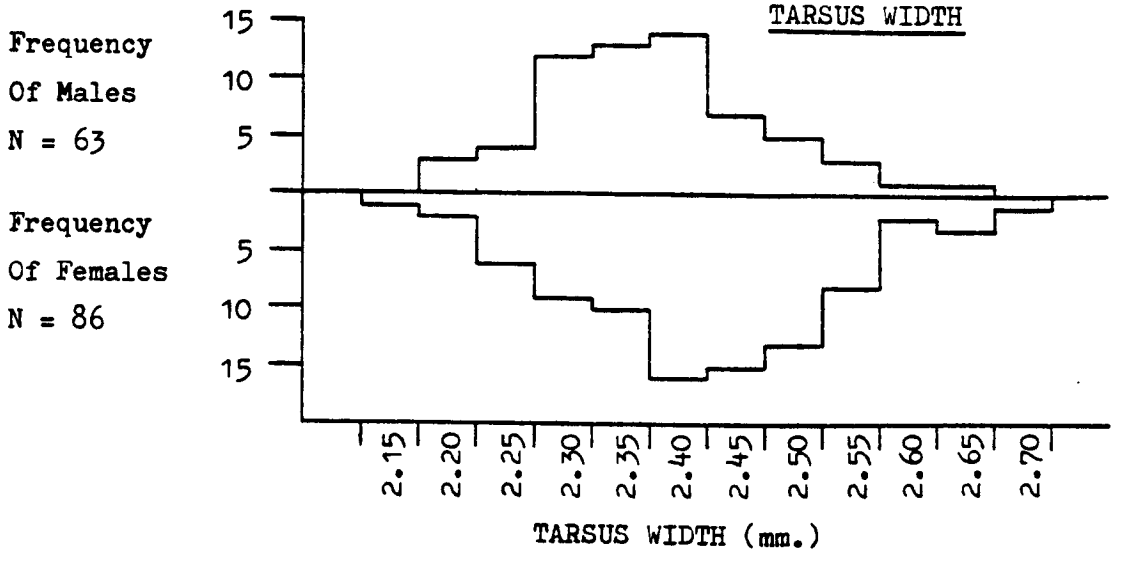
Sexing Individuals Never Caught In A Pair.

If a cloaca measurement was available, individuals of less than 4.0mm. were classed as males and those of greater than 4.0mm. as females. With no such measure, or one equal to 4.0mm., the weight was considered, and those of less than 131.0g. were classed as males, and those of more than, or equal to 131.0g. , as females.

This regime largely removed the subjectivity of sexing individuals. The determination for any bird was more likely to be accurate if it was from within a 'pairing complex', and least accurate at the individual level.

Fig. 3.5 The Frequency Distribution Histograms Of The Male And Female Measurements.

Only the last measurements of birds sexed by the 'M.E.V. method' are included.



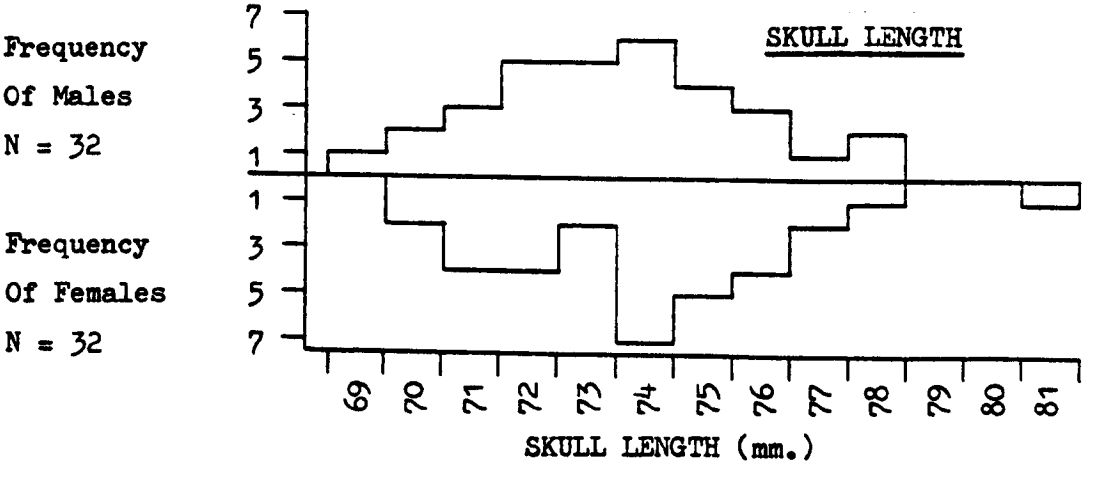
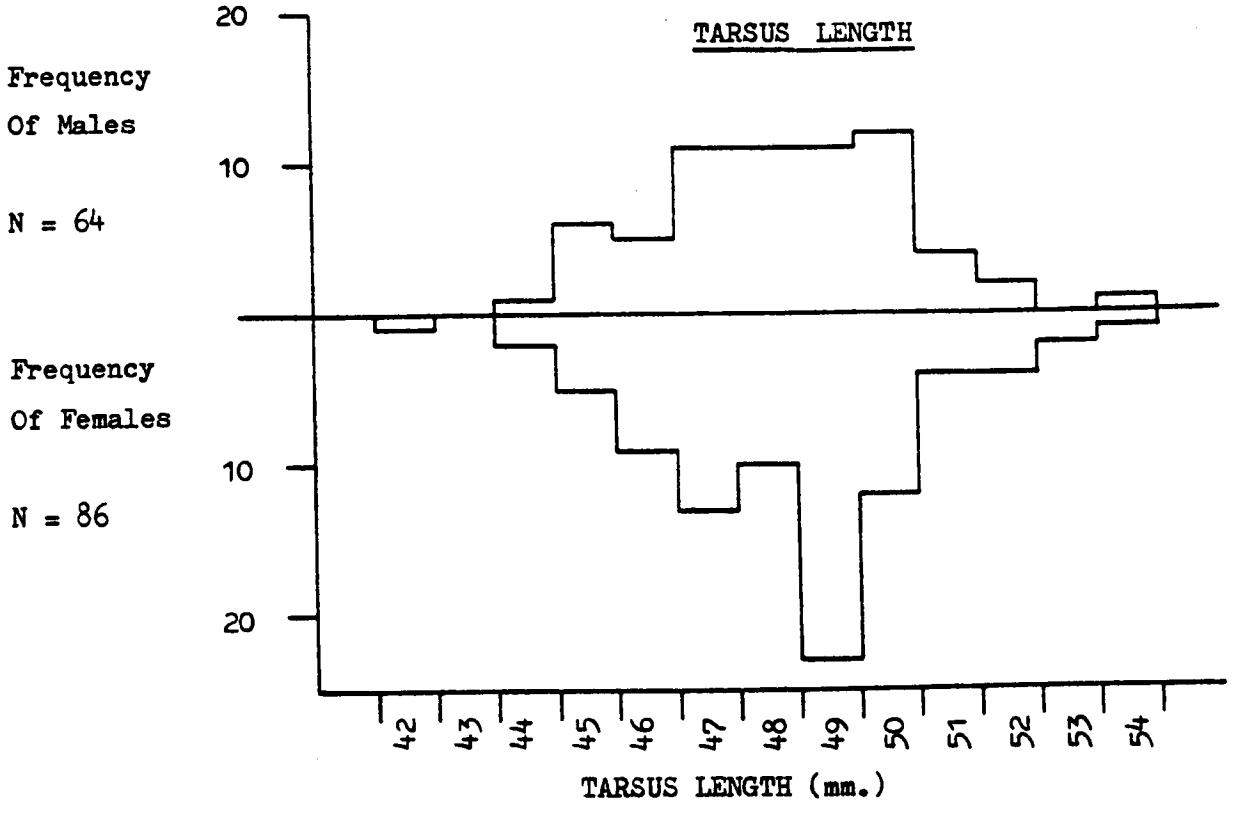


Fig. 3.5 (continued)



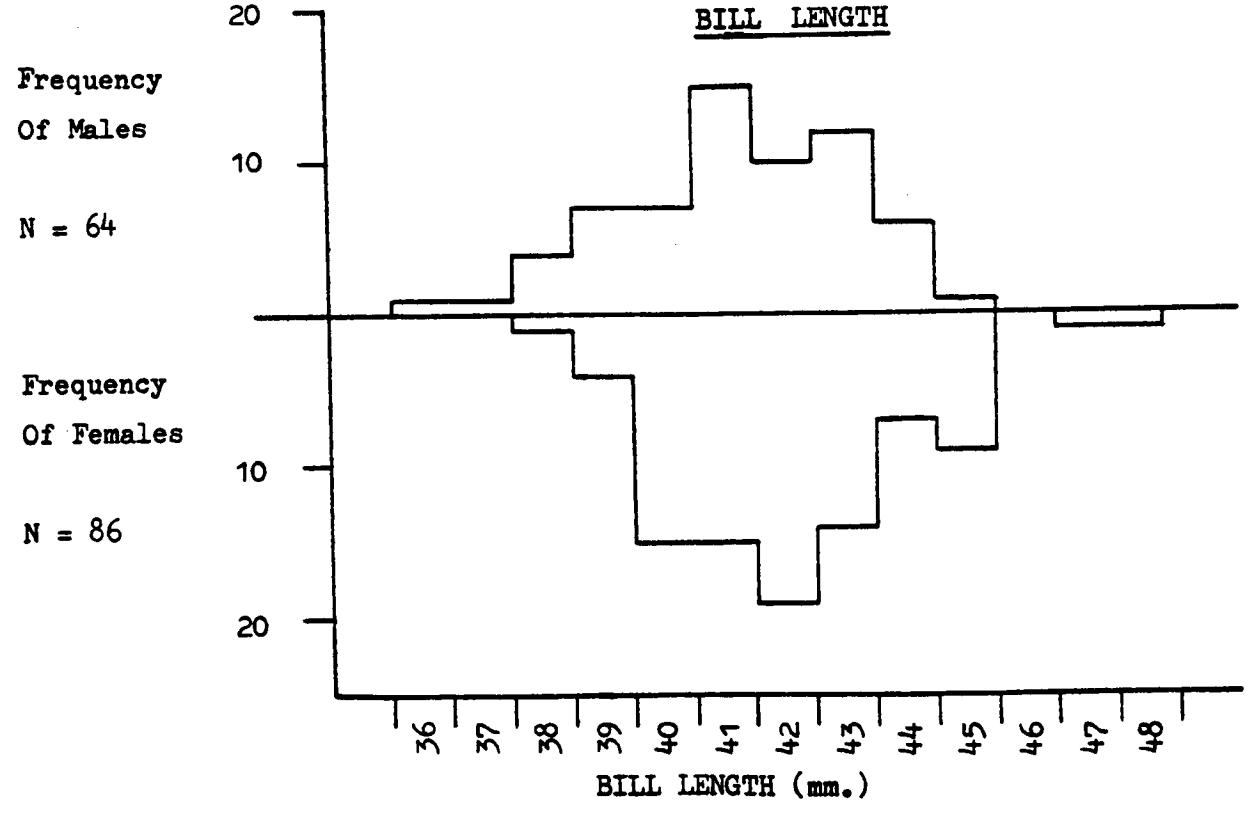
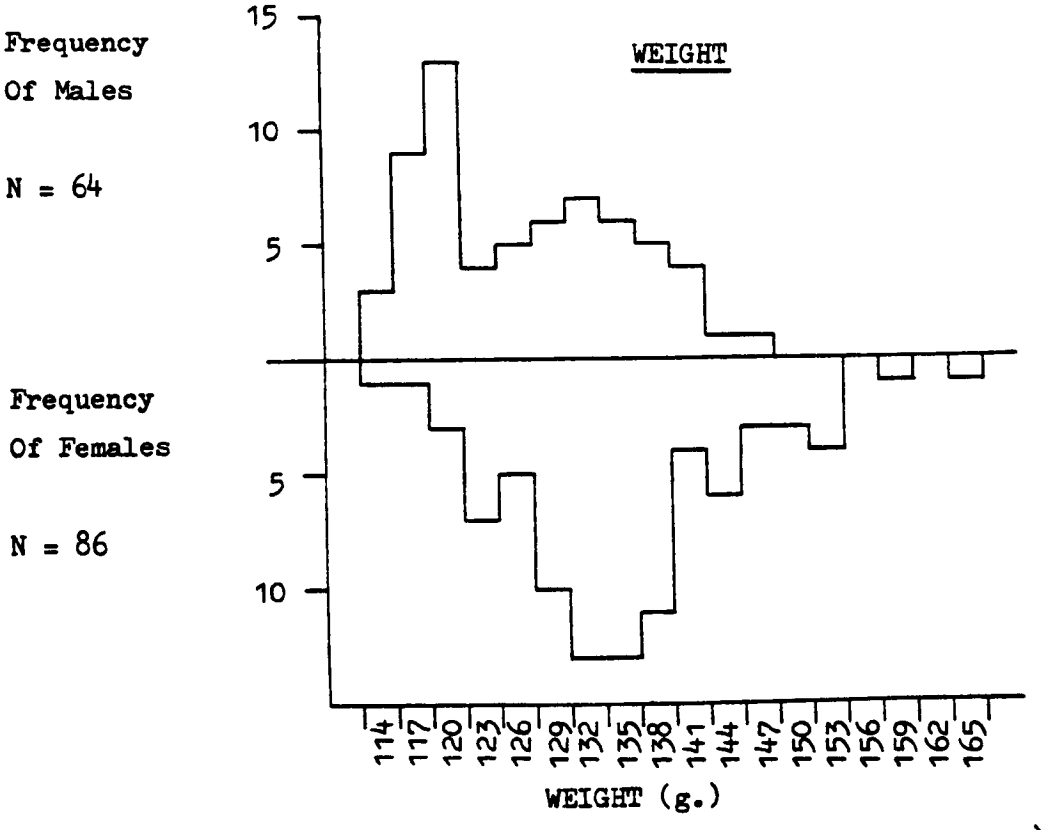


Fig. 3.5 (continued)



(the values are the highest of the class)

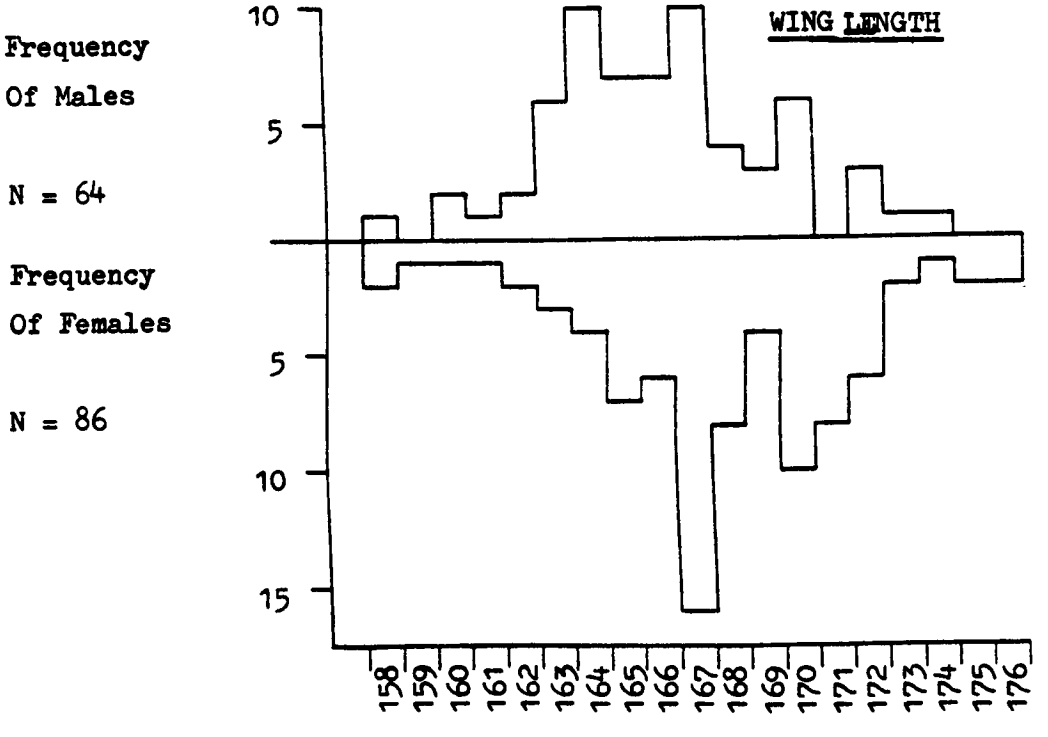


Fig. 3.5 (continued)

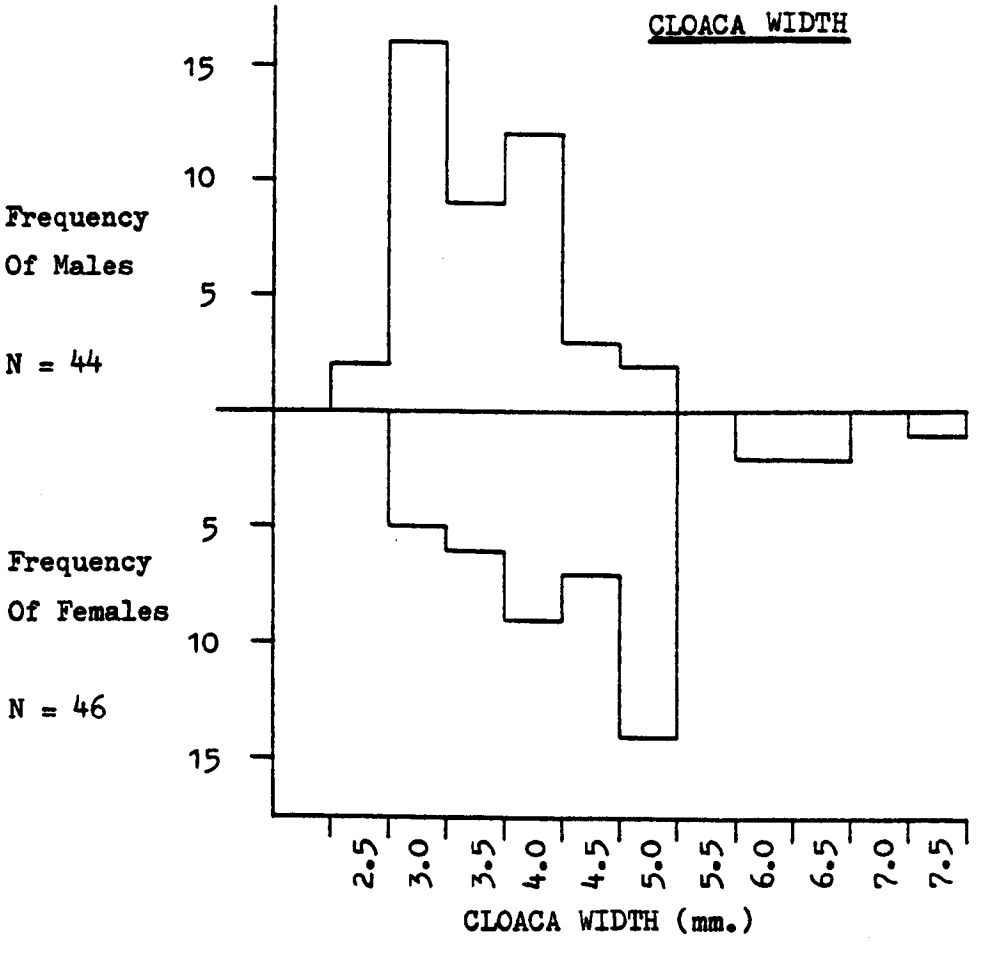


Table 3.2 A Summary Of The Distribution Of Cloaca Widths Among Birds Sexed By The 'M.E.V. Method'.

Fig. 3.5 showed the cloaca width to be the measurement most influenced by the sex of the bird. This is analysed further below.

Cloaca width.	Males	Females
< 4.0 mm.	17	11
= 4.0 mm.	12	9
> 4.0 mm.	5	26
Total.	34	46

$\chi^2 = 14.47$ P(2 df.) = 0.001

There was a highly significant difference of cloaca width between males and females. 50% of male cloacas were less than 4.0 mm. (23.9% female), and 56.5% of female's were greater than 4.0 mm. (14.7% male).

Table 3.3 The Relative Sizes Of Members Of Pairs Sexed By The 'M.E.V. Method'.

From all of the birds sexed by the 'M.E.V. method' there were 128 different pairings. In each of these the measurements were simply compared, and the results are given below. Where a pair was caught on more than one occasion the mean measurements were compared.

	Males greater than Females	Males equal to Females	Males less than Females
Weight	31	5	92
Wing length	42	10	76
Bill length	44	25	59
Tarsus length	56	18	54
Tarsus width	46	3	79
Breeding plumage	59	3	66

The greatest separation of the sexes was by the measurement of weight, for which the female was the largest in 72% of pairs.

3.3.3 Mate Selection On The Basis Of Size.

By comparing the size of members of a pair Jehl (1970) demonstrated that there was some selection for mate on this basis, in two species of sandpiper & Grosskopf (1959) suggested (from just two observations) that small male Redshank mated with small females.

This investigation considered 128 pairs in which individuals were sexed by the 'M.E.V. method'. Where a pair was recorded together, for more than one season, the mean annual measurements were used.

Table 3.4 gives the full correlation analysis that indicated that there was no selection of mate on the basis of size.

Table 3.4 The Correlation Analysis Of Size Parameters Of Members Of Pairs Sexed By The 'M.E.V. Method'.

Using the same sample as in Table 3.3 the male and female sizes were compared by correlation analysis below.

Correlation coefficients, r.

FEMALE SIZE	MALE SIZE: Weight	Wing length	Bill length	Tarsus length	Tarsus width
Weight	0.127	-0.035	0.040	0.085	0.013
Wing length	0.071	0.120	0.066	0.123	0.056
Bill length	-0.139	-0.040	-0.055	-0.066	-0.035
Tarsus length	-0.004	-0.071	-0.023	0.090	-0.117
Tarsus width	0.010	0.007	-0.038	-0.002	0.138

At a probability level of 0.05 , with 125 df.,

$$r = 0.174$$

therefore, there was no significant correlation between the size of the male and his mate.

3.3.4 The Timing Of Breeding Within A Season.

The investigation of when, during a breeding season, an individual or pair started breeding was complicated by the replacement of nests (and broods) that were unsuccessful (see Section 2.3.5). Later in a season the data collected were less precise, since many of the nests were not definitely known to be first nests. Despite this, the effects of individual age, mate age and mate fidelity were considered in relation to the starting of breeding (the date of clutch completion of the first known nest).

The analysis was not by parametric methods because Section 2.3.2 showed the timing of nests did not follow a normal distribution.

Individual age.

The age of individuals (taken as the number of years from first ringing as a breeding adult + 1) was most accurately estimated in the final years of this study, after many years of ringing. Only 1980 and 1981 were, therefore, considered.

Fig. 3.6 shows the distribution of the age and sex classes in three more or less equal periods during the breeding season. From this it is clear that few young birds (= first time recorded breeding), and most older birds bred early in the season. This is shown to be statistically significant in Table 3.5 .

It was probable that many of the old individuals breeding late in the season were from replacement nests.

In contrast to this result, the pulli known to have returned and bred in their first year are seen, in Table 5.8, to be capable of breeding early in the season.

Fig. 3.6 The Influence Of Individual Age On The Timing Of Breeding.

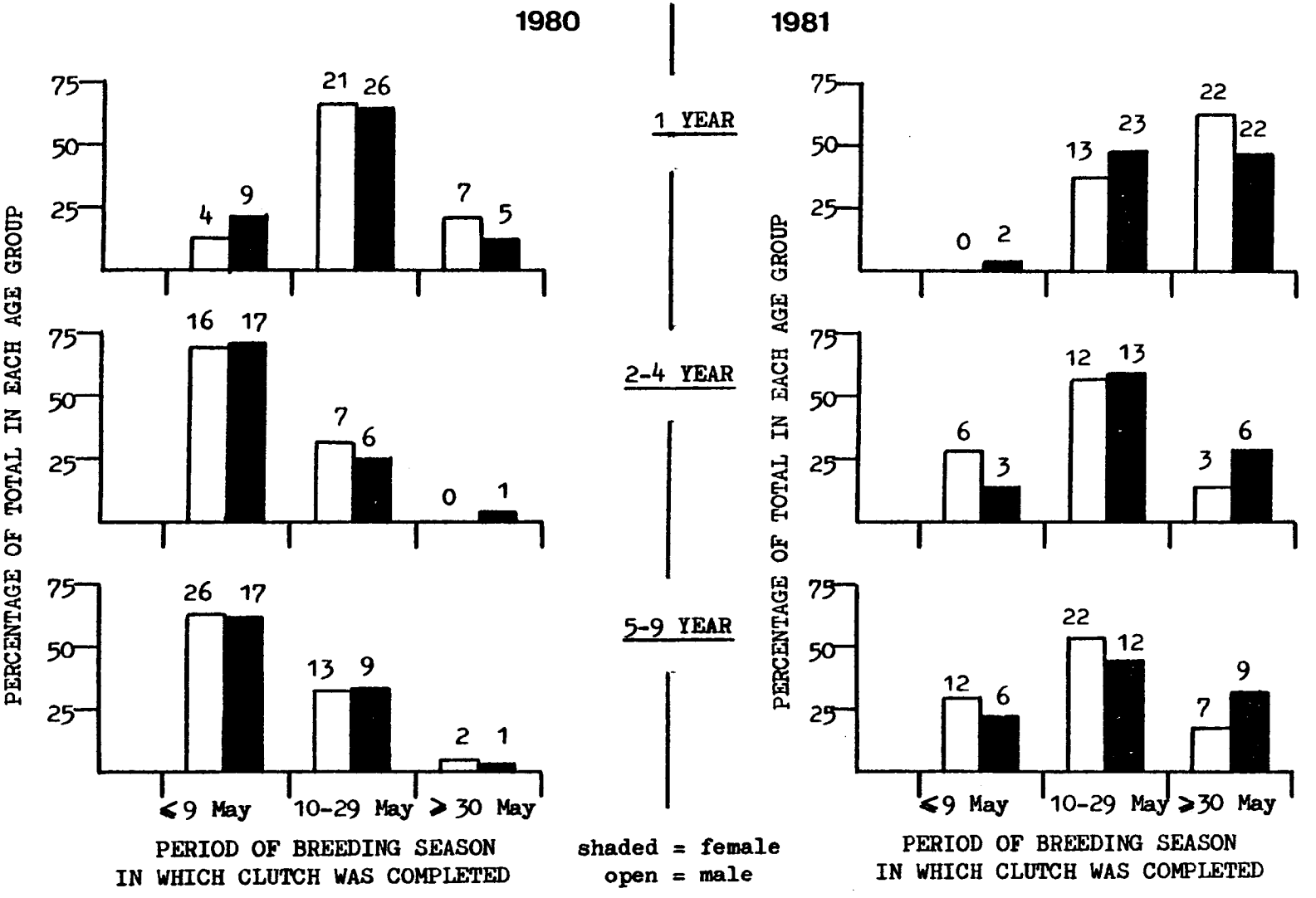


Table 3.5 The Influence Of Individual Age On The Timing Of Breeding.

Individual age was best estimated by the time from first capture, in the last years of the study. Two periods of clutch completion, early (before 10th. May) and late (after 9th. May), and two ages, young (first year of capture) and old (captured in a previous year), were considered in a chi-square analysis.

1980

MALES

Time	Young	Old
Early	4	42
Late	28	22
Total	32	64

$\chi^2 = 24.13$

$P(1 \text{ df.}) < 0.001$

FEMALES

Time	Young	Old
Early	9	34
Late	31	17
Total	40	51

$\chi^2 = 17.54$

$P(1 \text{ df.}) < 0.001$

1981

MALES

Time	Young	Old
Early	0	17
Late	35	45
Total	35	62

$\chi^2 = 11.64$

$P(1 \text{ df.}) < 0.001$

FEMALES

Time	Young	Old
Early	2	9
Late	45	40
Total	47	49

$\chi^2 = 4.71$

$P(1 \text{ df.}) < 0.05$

In both years analysed, for both sexes, the birds breeding for the first time did so later in the season than the older ones.

Mate age.

The young birds were divided into those with mates of the same age and those with older mates, and the timing of breeding is compared in Table 3.6 . The young males that bred early in the season tended to pair with older females (this was not similarly shown for the young females).

Mate fidelity.

In considering the influence of mate fidelity on the timing of breeding it was necessary to use only the males captured with their mate in successive years (see Section 3.3.6). This reduced the available data, such that there was only a sufficient sample from 1980.

Using the same periods as above, Table 3.7 shows that there was no large scale influence of mate fidelity on the timing of breeding of males. A more detailed consideration of the early period (before 10th May, that is , the 'first peak' of 1980) in Table 3.8 also revealed no significant influence of mate fidelity.

Overall, therefore, the young adults started breeding later in a season than the birds that had been recorded breeding in a previous season. The young males that did breed earlier, however, were more likely to pair with older females, probably because there were few young females 'available' at this time. There was no influence of mate fidelity on the timing of breeding that could be determined.

Table 3.6 The Influence Of Mate Age On The Timing Of Breeding Of Young Birds.

The same definitions as in Table 3.5 were used for early and late periods, and for young and old birds.

1980 YOUNG MALES

Time	Mate Age: Young	Old
Early	3	3
Late	15	3
Total	18	6

Fisher's Exact Probability = 0.017

YOUNG FEMALES

Time	Mate Age: Young	Old
Early	3	4
Late	15	9
Total	18	13

Fisher's Exact Probability = 0.18

1981 YOUNG MALES

Time	Mate Age: Young	Old
Early	8	0
Late	18	2
Total	26	2

Fisher's Exact Probability = 0.50

YOUNG FEMALES

Time	Mate Age: Young	Old
Early	8	5
Late	18	5
Total	26	10

Fisher's Exact Probability = 0.17

In 1981 the sample of old females paired with young males was very small (only 2, probably because of their lower nest site fidelity). However, in 1980 the young males that did breed early, were more likely than old males, to pair with older females. This was not so for young females.

Table 3.7 The Influence Of Mate Fidelity On The Timing Of Breeding Of Males Throughout The 1980 Season.

The fidelity of males captured, together with their mates, in 1979 and 1980, was compared to two classes of the timing of clutch completion in 1980 (early = before 10th. May, and late = after 9th. May).

	Faithful Males	Unfaithful Males
Early	9	7
Late	6	4
Total	15	11

Fisher's Exact Probability = 0.31

Therefore, there was no significant large scale influence of mate fidelity on the timing of breeding of males.

Table 3.8 The Influence Of Mate Fidelity On The Timing Of Breeding Of Males Within The 'First Peak' Of 1980.

Dates of clutch completion (days from 31st. March) and their associated ranks.

Unfaithful Males.	Date	26	28	29	31	32	33	33	
	Rank	2	3	4.5	8	10.5	13.5	13.5	
Faithfull Males.	Date	24	29	30	31	31	32	33	33	34
	Rank	1	4.5	6	8	8	10.5	13.5	13.5	16

Wilcoxon-Mann-Whitney Two Sample Test.

$N_1 = 7$ $N_2 = 9$ $T = 55$ $P > 0.05$

This demonstrates that for the year with the best available data, there was no significant effect of mate fidelity of males on the timing of breeding within the first peak.

3.3.5 Nest Site Fidelity.

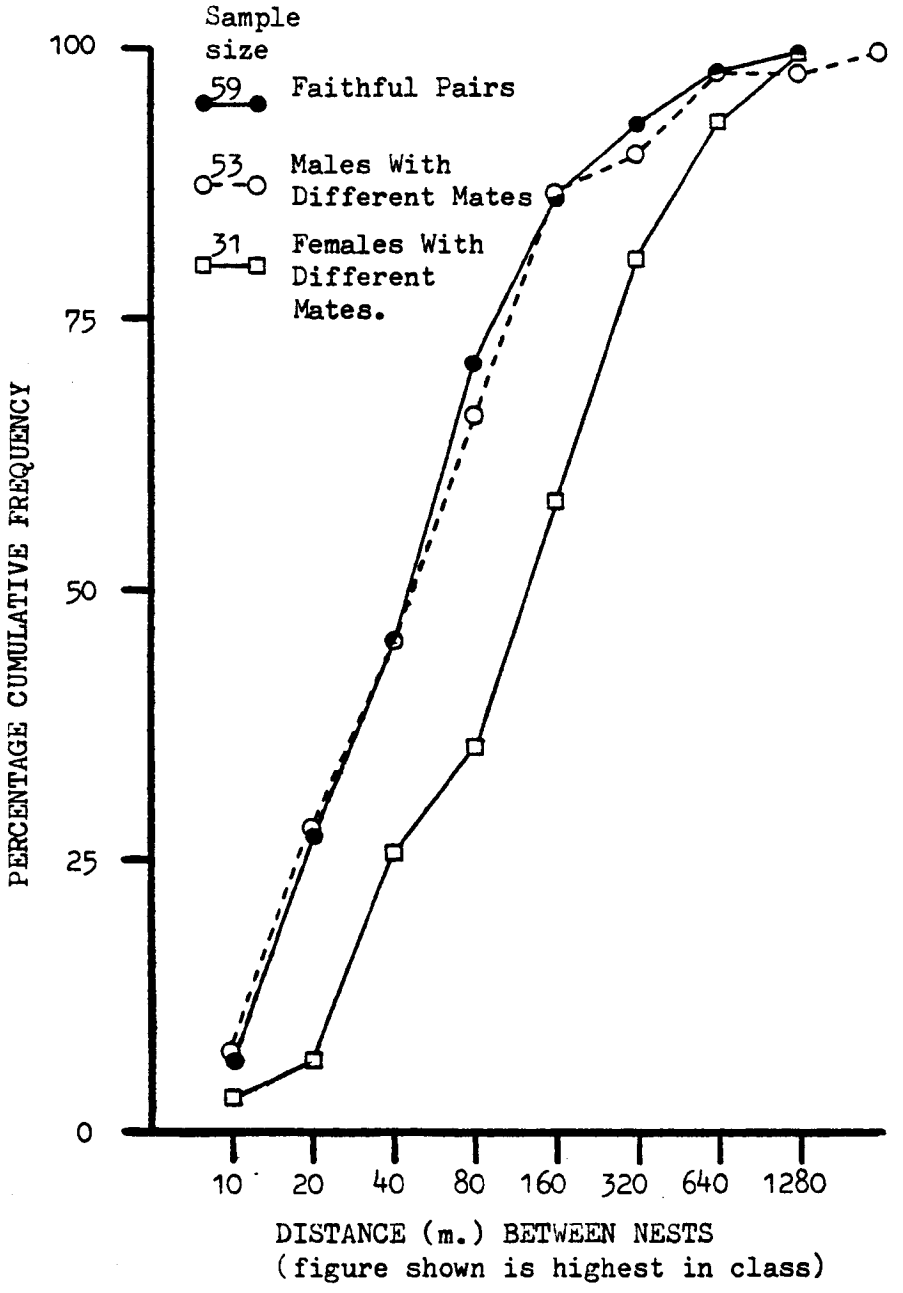
The determination of the degree of nest site fidelity, between years, was important in considering the results of the capture - recapture analysis (of Section 3.3.6). If individuals were highly mobile (that is, a low degree of nest site fidelity), the population studied would have indistinct boundaries, and a large proportion of the estimate of mortality would be due to emigration.

In considering the distance between nest sites it was thought necessary to use two strict criteria to improve the precision of any conclusions. Firstly, only the distance between nests of trapped pairs was used to determine any effect of mate faithfulness, and, secondly, only nests in consecutive years were used to eliminate any cumulative trends, and effect of unknown pairings.

Three classes of mate faithfulness were recognised, and Fig. 3.7 shows the frequency distributions and comparisons of the distances between nests, for each. There was no significant difference in the distance between nests in successive years of faithful pairs (median - 42m.) and unfaithful males (median - 55m.). However, there was a significant difference between unfaithful males (median - 55m.) and unfaithful females (median - 137m.).

All median distances (that is, the distance within which half the sample was found) were underestimates, and the frequency distributions biased towards the shorter distances, because, in general the greater the distance between nests, the lower the chance of finding both nests. This resulted from the small size of the study area, and would have affected the estimates of the females more, because of their significantly greater movements.

Fig. 3.7 The Influence Of Mate Fidelity On Nest Site Fidelity.



Wilcoxon-Mann-Whitney Two Sample Tests.

Faithful pairs and males with different mates.

$T = 2814.5$
$U_T = 2994.5$
$O_T = 171.6$
$Z = 1.049$
$P = 0.147$

Males with different mates and females with different mates.

$T = 977$
$U_T = 1317.5$
$O_T = 107.9$
$Z = 3.156$
$P = 0.0008$

	mean(m.)	median(m.)
Faithful pairs	99.7	42
Males with different mates	111.2	55
Females with different mates	209.0	137

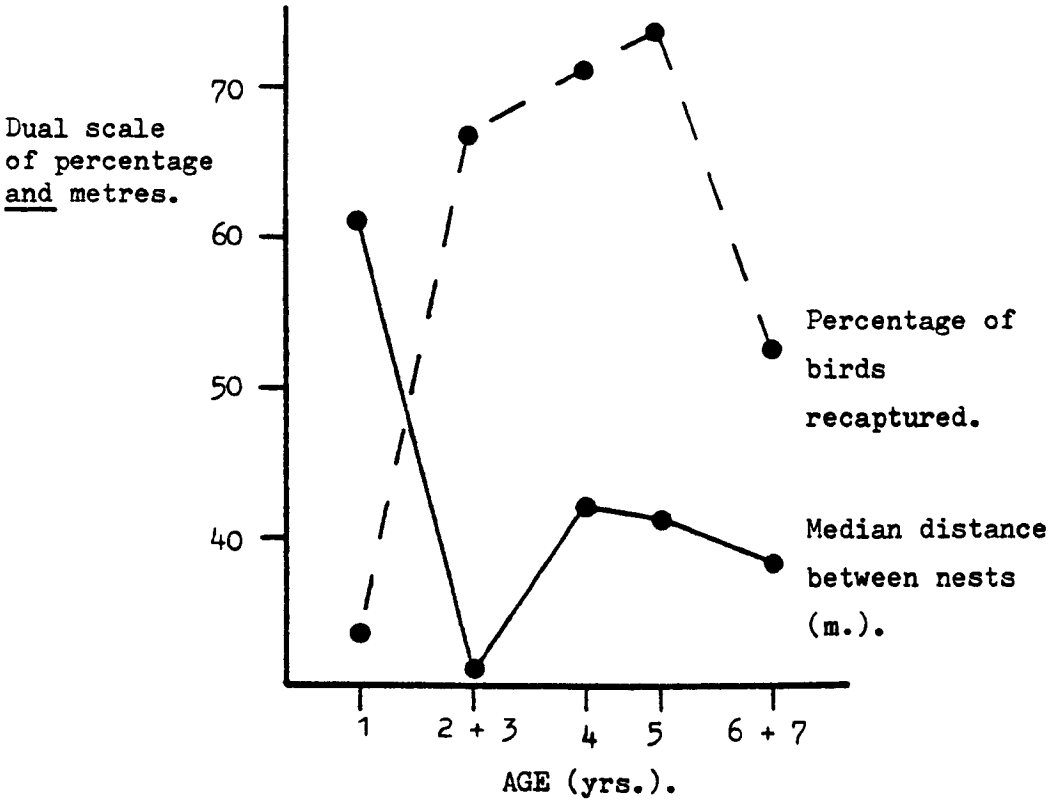
Further indication of this was found in the recapture rates in Table 3.9. The unfaithful females' rate of recapture was significantly lower than the unfaithful males'.

A lower return rate of young birds was found by Grosskopf (1959), but he was unable to determine if this was due to their lower survival rate or higher emigration. It is the influence of nest site fidelity on the different recapture rates of age groups (see Section 3.3.7) that I hope to elucidate.

The mate faithfulness of males did not effect their nest site faithfulness (see before), and so for this investigation of age, all males captured from 1978 to 1980, and recaptured in a following year, were used. The median distance moved between nests by males of different age groups, is shown, together with the percentage of recaptures in Fig. 3.8 .

There is some association between the two factors, but not enough for a significant correlation. The very low recapture rate of 'first year' birds is associated with a very high median distance between nests (61m.) . This great distance probably resulted in a greater emigration out of the study area, of young birds, where they would not have been available for recapture.

Fig. 3.8 The Influence Of Age On The Nest Site Fidelity Of Males.



There is some association between the factors of nest site fidelity and recapture rate for birds of different ages, but not sufficient for a significant correlation ($r = -0.75$, $P > 0.05$).

3.3.6 Mate Fidelity.

The effect of mate faithfulness on the distance between nest sites of an individual has already been shown (in Section 3.3.5), and its implication on the capture-recapture analysis (Section 3.3.7) noted. In its own right it is an interesting aspect of the breeding biology and this section considers the degree of fidelity to a previous mate between years, and within years.

Mate Fidelity Between Years.

The same strict criteria are used in this section as for studying nest site fidelity before. Table 3.9 shows that significantly fewer females (31) were recaptured if they changed mates, than were males (52). It has previously been shown (in Section 3.3.5) that females with new mates moved further between nests than males with new mates. Therefore, more females probably moved out of the study area, where they were not available for recapture, giving the above significant difference.

Mate fidelity was, therefore, investigated from the MALE aspect only, since their capture history was more accurately known and detailed, following their stronger nest site fidelity.

The estimate of annual mate fidelity, for surviving males, was determined from the totals of Table 3.9;

$$\text{estimate of annual mate fidelity} = \frac{\text{total pairs faithful}}{\text{total pairs faithful + males unfaithful}}$$

$$= \frac{62}{62 + 52}$$

$$= 0.544$$

Table 3.9 A Summary Of Mate Fidelity.

From all individuals captured, together with their mates, in two consecutive years, it was possible to draw up the following table that summarised mate fidelity. The analysis of the differences between the numbers of males and females with new mates is also shown.

Known outcome of pairs in the following year.	YEARS								
	1973	1974	1975	1976	1977	1978	1979	1980	Total
Faithful pairs.	1	2	8	2	8	11	15	15	62
Males with new mate.	0	4	4	4	3	6	11	20	52
Females with new mate.	0	2	1	1	3	5	4	15	31
Differences male - female (new mate only).		2	3	3	0	1	7	5	
Signed rank of difference.		+3	+4.5	+4.5	1	+2	+7	+6	

Wilcoxon's Signed Rank Test.

T- = 0 T+ = 27 P = 0.02

Therefore, significantly fewer females were recaptured, if they changed mates, than were males.

The fate of breeding pairs in the following breeding season was also investigated in Fig. 3.9 , using the mortality estimate of Section 3.3.7 , and the above estimate of mate fidelity. This demonstrates that 42% of pairs in one year, were faithful in the next. However, the more usual presentation of such results expresses the mate fidelity of pairs in which both individuals survive; this was 71% (42% divided by 59%).

The estimate that 46% of surviving males paired with a new mate in the following year did not distinguish between death, emigration, or , a true 'divorce' of mate (where pairing occured with another mate, despite the prescence of the old mate on the breeding area). To investigate this, the fate of MALES from known females with new mates is used as the most reliable indicator of true 'divorce', because of the males greater nest site fidelity.

Thirty-one cases of change of mate between successive years were observed for females (see Table 3.9). Fourteen of the males of the original pairings were recorded breeding subsequently. That is,

$\frac{14}{31} = 0.45$ of pairs known to have split up were true 'divorces'.

However, this estimate must be considered together with the following. Firstly, the recording of a male breeding subsequently did not necessarily mean it was available to pair with when the female was observed with a new mate. Secondly, the above figure probably underestimated the true value, since the number of males sampled only averaged 0.36 of the estimated total population (see Table 3.21).

These are overall results for the population, but at the individual level there were differences. Two aspects are considered

Fig. 3.9 A Model Of Mate Fidelity.

The ANNUAL MORTALITY of both sexes is estimated at 0.23

The MATE FIDELITY of surviving males is estimated at 0.54 [A]

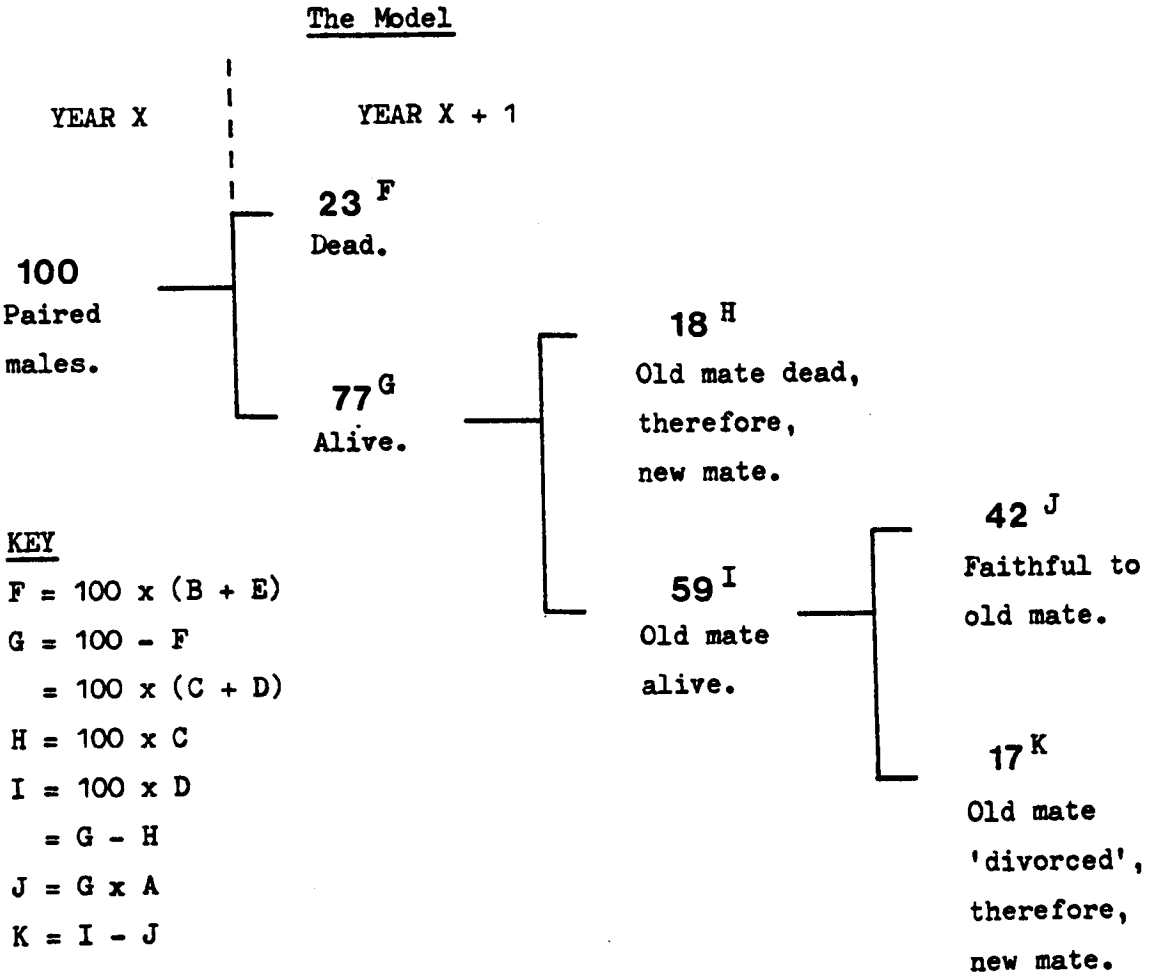
From the annual mortality, above, a 'PAIR MORTALITY' is calculated;

P(only male dying) = 0.23 x 0.77 = 0.18 [B]

P(only female dying) = 0.77 x 0.23 = 0.18 [C]

P(both surviving) = 0.77 x 0.77 = 0.59 [D]

P(both dying) = 0.23 x 0.23 = 0.05 [E]



below.

The influence of previous mate history on subsequent mate faithfulness.

To investigate whether a pair faithful from the previous year was more likely than a new pairing, to remain together in the next year, the males captured together with their mate in three consecutive years were analysed. Table 3.10 shows that the previous pairing did significantly affect a future one, such that if a pair had been faithful for one year, it was more likely to be faithful in the following, than was a new pair. This factor probably accounted for the many observed cases of mate faithfulness lasting for many years.

The influence of breeding success on subsequent mate faithfulness.

It was considered that successful breeding might increase a pairs chance of remaining faithful, but the data available of nesting success, in Table 3.11 , did not support this, although nesting success may not be a good indicator of breeding success.

In agreement with Grosskopf (1959) this study has revealed two cases of'divorce', followed by renewed faithfulness; this will be discussed later.

Mate Fidelity Within Years.

Fourteen males were caught on two nests, together with their mates, within the same year. Of these, three had changed mates, thus

$\frac{3}{14} = 0.24$ was the 'divorce' rate within a year.

However, this assumed that all of the first mates were available for renesting. Two observations indicated that this was not so.

Table 3.10 The Influence Of Previous Faithfulness To A Mate On Future Faithfulness To That Mate.

From the males captured, together with their mates, in three consecutive years, it was possible to determine the above factor in mate fidelity. In the 2x2 contingency table below, same and different mate refer to the intermediate year.

MATE IN PREVIOUS YEAR.	MATE IN FOLLOWING YEAR.	
	Same Mate	Different Mate
Same Mate	7	7
Different Mate	1	9
Total	8	16

Fisher's Exact Probability. = 0.047

Therefore, the previous pairing history of males did significantly influence the choice of a future mate, such that, if a pair had been faithful for one year already, it was more likely to be faithful in the following year, than was a new pair.

Table 3.11 The Influence Of Nest Outcome On Mate Faithfulness In The Following Year.

The mate faithfulness of the males captured, together with their mates in two consecutive years (from 1979 to1981), is compared by the outcome of the nests in the first year.

Outcome of nest.	Faithful pairs.	Males with different mate.
Hatched	17	21
All eggs addled	5	3
Crushed	1	1
Trapping loss	4	5
Flooded	1	1
Deserted	1	0
Predation loss	0	1
Total	29	32

Without further analysis it was clear that the nest outcome in one year had no effect on the mate fidelity of males in the next year.

Firstly, there was a single case of a male renesting with a new mate, while the original female continued to incubate and hatched the first clutch, that is, polygyny. The first egg of the second clutch was estimated to have been laid eleven days before the first clutch hatched.

Secondly, close observation of a nest in 1981 (by J.Selman) revealed that an individual incubated, and reared the chicks to at least ten days, alone. The desertion by its mate apparently followed the partial predation of the clutch.

The 'divorce' rate within years, 0.24, was very similar to that calculated for between years, 0.29 (both members of pair alive).

3.3.7 The Estimation Of Annual Mortality And Population Size.

With an annual sample of the breeding population, individually marked and released, the demographic parameters of mortality and population size is estimated with a multiple capture-recapture model. The methods considered were those of Manly and Parr (1968), Jolly (1965), and Fisher and Ford(1947).

The Fisher and Ford (1947) method assumes the survival rate to be both constant and age-independent, and these were found not to apply to this population (see later). The Manly and Parr(1968) method requires a very large, extensive sample for each year, and this was not available. The Jolly stochastic method (1965) was,therefore, the only remaining method, and its use was considered appropiate for this population (see later).

There was one major violation of the method's assumptions, and this was with respect to the lower 'survival' rate of the birds breeding for the first time (see later). However, Seber (1973, p.232) stated that, "if survival is independent of mark status and probability of capture independent of age, the Jolly (-Seber) method will not be greatly affected by age-dependent mortality". The first two assumptions above, are both seen to hold (later), and so the use of this model is considered valid.

Testing The Assumptions Of Jolly's Stochastic Method (1965).

As briefly discussed above, this method is a mathematical one, giving mathematical answers that are only comparable with the biological answers if the strict assumptions of the method are largely adhered to. These are considered in detail below.

All marks were permanent, and noted correctly on recapture.

Metal rings have long been used to identify birds individually and they have been seen to have very little effect on them. Although ring loss has been considered to affect the accuracy of survival estimates in birds (for example, Coulson 1960 and Grosskopf 1964) this has mainly concerned the use of soft alloys. In this study rings of the hard alloy 'monel' were used, which, even after eight years showed little wear, and all identification numbers were read. The addition of colour rings provided a check on actual ring loss, and there was no case of a bird, with colour rings, having lost its metal one (sample size was 625 birds and 561 recaptures)

All individuals, whether marked or not, had an equal chance of being caught.

Table 3.12 shows that significantly fewer females were recaptured than males, but this does not differentiate between death or emigration. It was clear from the analysis of nest site fidelity (in Section 3.3.5) that females, on changing mate, were more likely than males to emigrate from the study area. The sexes were, therefore treated as distinct sub-groups, and analysed separately.

Random sampling, within a sub-group (sex), is investigated with the test given by Leslie (1958). This ideally requires a sample of more than twenty birds known to have survived a single period of more than three years. The data set that provides the best fit to these criteria is for the males caught in 1976 and recaptured in 1981, that is, 19 individuals with a chance of being caught in four

Table 3.12 The Analysis Of Differences In Recapture Rates Between The Sexes.

The sexes were compared, each year, by chi-square analysis, on the basis of whether or not they were recaptured since their capture.

YEAR		MALES	FEMALES	χ^2	P(1 df.)
1980					
	Recaptured	43	32		
	Not recapt.	53	59		
	Released	96	91	1.80	< 0.25
1979					
	Recaptured	43	29		
	Not recapt.	26	35		
	Released	69	64	3.87	< 0.05
1978					
	Recaptured	45	37		
	Not recapt.	30	40		
	Released	75	77	2.18	< 0.25
1977					
	Recaptured	25	23		
	Not recapt.	26	28		
	Released	51	51	0.16	> 0.05
1976					
	Recaptured	48	27		
	Not recapt.	34	41		
	Released	82	68	5.27	< 0.025

Table 3.12 (cont.)

YEAR	MALES	FEMALES	χ^2	P(1 df.)
1975				
Recaptured	40	31		
Not recapt.	28	35		
Released	68	66	1.89	< 0.025
1974				
Recaptured	32	30		
Not recapt.	34	36		
Released	66	66	0.12	> 0.05

In all years, fewer females were recaptured than would have been expected if there was no difference between the sexes. Therefore, the chi-square values, and their associated degrees of freedom, were added to provide an overall figure;

$$\text{Total } \chi^2 = 15.29 \text{ (with 7 df.)}$$

$$P < 0.05$$

that is, overall significantly fewer females were recaptured than males.

Table 3.13 Analysis, By The Method Of Leslie (1958), Of Males Released In 1976 And Recaptured In 1981, For Random Sampling In The Intervening Years.

Number of captures per individual. (x)	Frequency. (f)	fx	fx^2
0	2	0	0
1	8	8	8
2	5	10	20
3	3	9	27
4	1	4	16
Total	19	31	71

Actual sum of squares

$= 71 - \frac{31^2}{19}$

$= 20.42$

Year	Number of recaptures each year. (n_i)	$(n_i)^2$
1977	2	4
1978	8	64
1979	7	49
1980	14	196
Total	31	313

Expected variance

$= \frac{31}{19} - \frac{313}{19^2}$

$= 0.765$

$$\chi^2 \equiv \frac{20.42}{0.765} = 26.69 \quad \text{(with 18 df.)}$$

$$P \triangleq 0.10$$

Therefore, even though the sample was small, the hypothesis that sampling, within the sub-group of males, was random, is supported.

years. The analysis is given in Table 3.13 and supports the hypothesis that sampling, within the sub-group of males, was random.

If all of the available captures were used in the analyses there would have been some areas not sampled in some years (see Fig.2.2). Therefore, all individuals did not have an equal chance of capture in all years. To rectify the violation of this present assumption, it is necessary to utilise a sub-sample from an area covered in all years. This was termed the Restricted Area (see Section 2.3.1), within which, from 1974 to 1981, all birds were considered to be equally available for capture.

This obviously reduced the available sample, but in addition to fulfilling the assumption, increases the significance of the results, for example the population estimate is now linked with a definate area.

<u>The capturing, handling and marking, one or more times, of an individual had no effect on its subsequent chance of recapture.</u>

The effect of the initial marking is investigated by determining if those marked for the first time were recaptured as frequently as those already captured and marked. In this analysis it is important to remove any influence of age (see later), and this is largely acheived by investigating only the very early years of the study. Then, because of the small proportion of the population already captured, an unringed bird was probably not a young bird. This contrasted with the last few seasons, when an unringed bird could be more confidently aged as a young bird. The analysis is given in Table 3.14.

Some individuals might have been either 'trap shy' or the

Table 3.14 The Analysis Of Initial Marking 'Mortality'.

It was important to reduce the effect of age (see Table 3.17), so only the earlier years of the study were investigated (1975 and 1976). The birds first captured in these years were less likely, than later years, to be young ones.

	Captured after 1975	Not captured after 1975
First captured in 1975 and released.	33	22
Recaptured in 1975 and released.	7	6
Captured in 1975 and released.	40	28

$\chi^2 = 0.16$ (with 1 df.)

$P > 0.25$

	Captured after 1976	Not captured after 1976
First captured in 1976 and released.	28	24
Recaptured in 1976 and released.	19	11
Captured in 1976 and released.	47	35

$\chi^2 = 0.70$ (with 1 df.)

$P > 0.25$

These two years results indicated that being caught and marked for the first time did not affect the birds significantly.

reverse, and therefore the chance of capture would have been affected by their capture history (that is, their mark status). Table 3.15 showed the analysis of the males captured in 1980.

These two analyses, above, indicated that there was no significant influence on recapture of the initial marking, and that it was not significantly dependent upon mark status.

The capturing, handling and marking one or more times, had no effect on an individuals chances of dying or emigrating.

Generally, this could not be tested, but since all marked individuals have been shown (above) to be equivalent, irrespective of the number of captures, it is reasonable that this assumption held.

The effect of patagial wing tags on survival could be analysed, because a sample was marked in 1980. Recaptures of these are compared, in Table 3.16, to recaptures of those not tagged in the same year. There was not a significant effect on the chances of recapture, one year later, caused by the fitting of patagial wing tags to males older than one year.

The age of birds did not affect their chance of recapture.

The age of birds could only be estimated from the time since their first capture. Following the small proportion of birds captured annually (from Table 3.21, male average was 0.36, and from Table 3.22, female average was 0.26, of the total estimated population) the estimate of ages within the population was most accurate in the final years of the study. The years from 1978 to 1980 are , therefore,

Table 3.15 The Analysis Of The Dependence Of Recapture On The Mark Status.

To remove the effect of the low recapture rate of young birds (see Table 3.17), those caught for the first time were not included. The chance of recapture of males caught in 1980 was compared with their capture history.

1980 MALES. Times caught previously.

	1	2	3	4	Total
Recaptured	11	9	7	7	34
Not recaptured	8	9	9	4	30
Released	19	18	16	11	64

$\chi^2 = 1.35$ (with 3 df.)

$P > 0.75$

Therefore, there was no significant dependence of the chance of recapture of males upon their mark status.

Table 3.16 The Analysis Of The Effect Of Patagial Wing Tags On The Recaptures Of Males In 1981.

The recaptures of all males, older than one year, captured in 1980, were analysed for the effect of the patagial wing tags that were fitted to some of them.

	Wing tagged	Ringed only
Recaptured	21	14
Not recaptured	20	10
Released	41	24

$\chi^2 = 0.308$ (with 1 df.)

$P > 0.1$

Therefore, the fitting of patagial wing tags to males did not significantly effect their chance of recapture.

investigated for subsequent recaptures of different aged birds.

The recapture rates for the two sub-groups (sexes) are shown, in Fig. 3.10 , and in Table 3.17 the analyses of recaptures of 'first year' and 'older' birds, are given. The 'first year' birds, of both sexes, were highly significantly less likely to be recaptured than older ones. In Fig. 3.9 the proportion of recaptures of 'first year' males was approximately half that of older ones.

Some of this discrepancy is due to the lower nest site fidelity shown by the younger males (see Section 3.3.5), that would have resulted in their greater emigration. However, a difference in survival between young and old breeding adults cannot be ruled out.

Sampling periods were short in relation to the total time.

The duration of the sampling of adults in the years from 1974 to 1981 is shown in Table 3.18 . The mean duration of the sampling period was 62 days, which was considered an acceptably small proportion of the total time (17% of one year).

Fig. 3.10 The Influence Of Age On The Recapture Rates Of Males And Females.

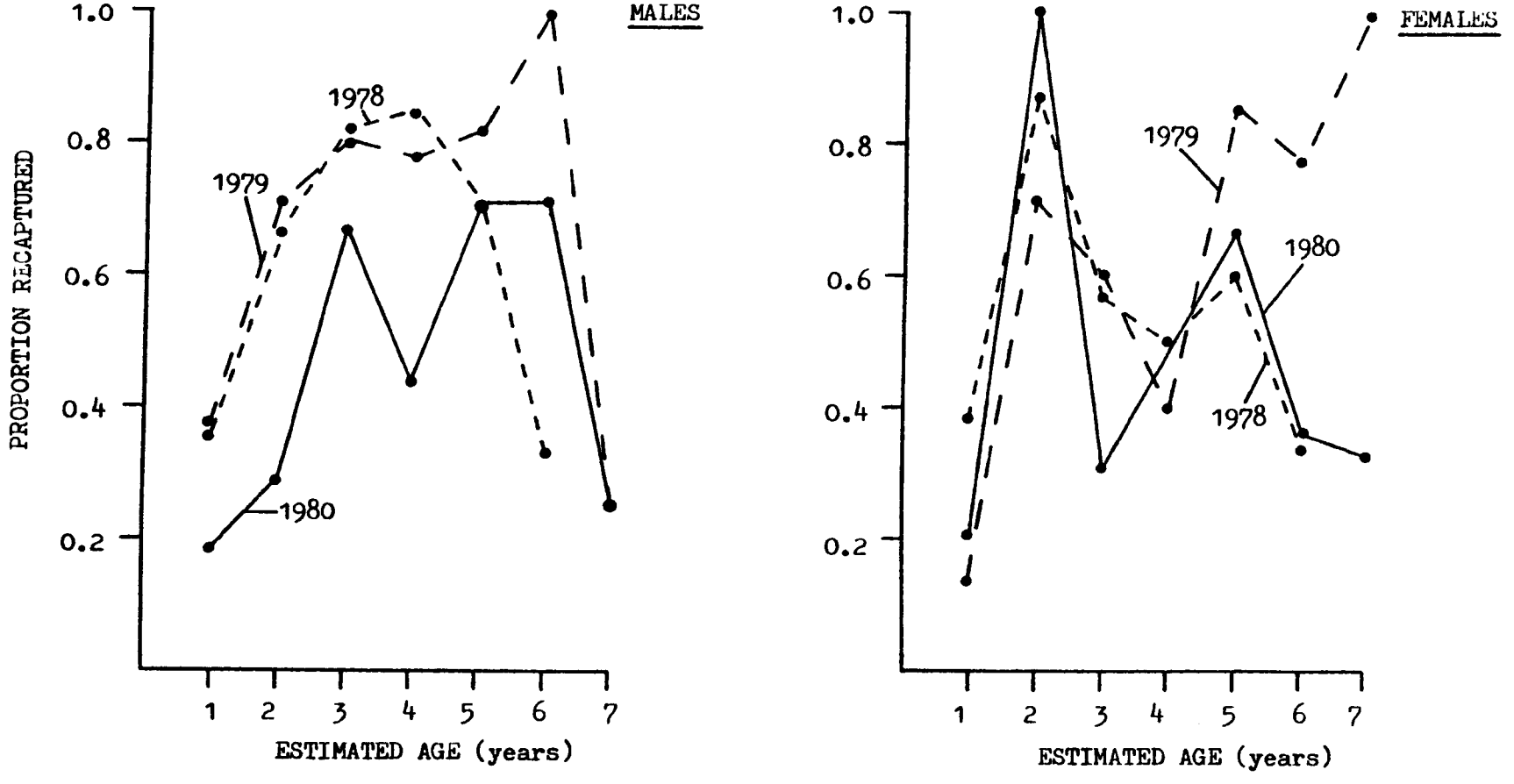


Table 3.17 The Analysis Of The Recaptures Of First Year And Older Birds.

First year birds, in the last three years of the study, were considered to be those caught for the first time. The recaptures of the sexes were treated separately, and the first year and older birds were compared.

MALES

Year	1978		1979		1980	
Age	1st y.	Old.	1st y.	Old.	1st y.	Old.
Recaptured	10	35	10	33	9	34
Not recaptured	18	12	16	10	23	30
Released	38	47	26	43	32	64
χ^2	8.09		10.11		5.08	
P(with 1 df.)	< 0.005		< 0.005		< 0.025	

Total $\chi^2 = 23.28$ (with 3 df.)

$P < 0.001$

FEMALES

Year	1978		1979		1980	
Age	1st y.	Old.	1st y.	Old.	1st y.	Old.
Recaptured	16	21	4	25	8	24
Not recaptured	26	14	25	10	31	28
Released	42	35	29	35	39	52
χ^2	3.67		21.26		6.43	
P(with 1 df.)	< 0.1		< 0.001		< 0.025	

Total $\chi^2 = 31.36$ (with 3 df.)

$P < 0.001$

Therefore, in both sexes first year birds were highly significantly less likely to be recaptured, than older ones.

Table 3.18 The Periods Of Trapping from 1974 to 1981.

Year.	Date of first capture.	Date of last capture.	Duration of trapping (days).
1974	1-5	1-7	61
1975	29-4	7-7	69
1976	4-5	12-7	69
1977	12-5	29-6	48
1978	5-5	27-6	53
1979	14-5	4-7	51
1980	24-4	30-6	67
1981	22-4	7-7	76

The mean duration of trapping was 62 days.

A Summary Of Jolly's Stochastic Model (1965).

Individuals were captured, marked, and released in i years, and the total number captured in any year was n_i . The recapture of each individual contributed only its most recent mark of release, m_i (not its complete capture history).

The estimation of the number of marked individuals in the population, M_i , was made by,

$$M_i = m_i + \frac{z_i(r_i + 1)}{(y_i + 1)}$$

where, z_i = the number of individuals marked before year i , not caught in year i itself, but caught subsequently.

r_i = the number of individuals released in year i .

y_i = the number of r_i that were caught again, subsequently.

The estimated population size, N_i , was determined by,

$$N_i = n_i + \frac{(n_i + 1)(r_i + 1)z_i}{(m_i + 1)(y_i + 1)}$$

$$= \frac{M_i(n_i + 1)}{(m_i + 1)}$$

and survival, from year i , to year i + 1 , s_i , by,

$$s_i = \frac{M_i + 1}{M_i - m_i + r_i}$$

The overall suvival rate was calculated as the geometric mean of all the individual annual survival rates, that is,

$$s_o = \sqrt[n]{s_1 + s_2 + \ldots\ldots s_n}$$ where n = number of rates.

The estimated number of additions to the population, between year i , and year i + 1 , B_i was made by,

$$B_i = N_{i+1} - s_i(N_i - n_i + r_i)$$

More complete explanations, together with the estimation of the standard errors can be found in Jolly(1965), Seber(1973), Southwood (1966) and Begon (1979).

The extracted data required for the analysis are given in Table 3.19 (males), and Table 3.20 (females), and the full results are given in Table 3.21 (males), and Table 3.22 (females).

Note on the use of standard errors.

The utilisation of the generated standard errors (and the subsequent confidence limits) has been seriously questioned by Manly (1971), and Roff (1973). They determined that the formulae for the calculation of the standard errors were questionable, and that the estimates and standard errors were highly correlated. Therefore, they are only given as a guide to the nature of the results.

Table 3.19 The Capture-recapture Data Of Adult Males For Analysis By The Method Of Jolly (1965).

Year i	Captured n_i	Year of release of marks, j						
		1974	1975	1976	1977	1978	1979	1980
		Recaptured marks, m_{ij}						
1974	66							
1975	68	12						
1976	82	6	21					
1977	51	5	8	13				
1978	75	7	5	16	15			
1979	69	1	2	6	6	23		
1980	96	0	1	9	4	16	32	
1981	97	1	2	2	0	6	8	42

Table 3.20 The Capture-recapture Data Of Adult Females For Analysis By The Method Of Jolly (1965).

Year i	Captured n_i	Year of release of marks, j						
		1974	1975	1976	1977	1978	1979	1980
		Recaptured marks, m_{ij}						
1974	66							
1975	66	7						
1976	68	8	14					
1977	51	6	5	6				
1978	77	5	1	10	15			
1979	64	0	6	3	3	16		
1980	91	3	3	4	2	16	20	
1981	96	1	2	1	0	5	9	29

Table 3.21 The Computations Of The Male Capture-recapture Data By The Method Of Jolly (1965).

*i	n_i	y_i	z_i	m_i	N_i	SE_{N_i}	s	SE_s	B_i	SE_{B_i}	$\frac{m_i}{n_i}$	$\frac{n_i}{N_i}$
1974	66	32										
							0.705	0.109				
1975	68	39	20	12	251.1	65.15					0.18	0.27
							0.815	0.104	44.9	57.0		
1976	82	46	32	27	249.5	43.57					0.33	0.33
							0.939	0.142	17.1	43.7		
1977	51	25	52	26	251.3	48.39					0.51	0.20
							0.640	0.098	11.2	24.2		
1978	75	45	34	43	172.0	22.93					0.57	0.44
							0.823	0.097	53.0	20.8		
1979	69	40	41	38	194.6	28.27					0.55	0.35
							0.754	0.091	15.2	15.7		
1980	96	42	19	62	162.0	20.18					0.65	0.59
1981	97			61							0.63	
										mean	0.49	0.36

Overall s = 0.774

Life Expectancy = 3.89 years

*see text for explanation of symbols.

Table 3.22 The Computations Of The Female Capture-recapture Data By The Method Of Jolly (1965).

* i	n_i	y_i	z_i	m_i	N_i	SE_{N_i}	s	SE_s	B_i	SE_{B_i}	$\frac{m_i}{n_i}$	$\frac{n_i}{N_i}$
1974	66	30										
							0.806	0.152				
1975	66	31	23	7	469.3	167.6					0.11	0.14
							0.966	0.185	-120.6	157.6		
1976	68	24	32	22	333.0	78.51					0.32	0.20
							0.727	0.161	88.08	72.5		
1977	51	20	39	17	330.0	84.86					0.33	0.15
							0.600	0.115	19.26	44.37		
1978	77	37	28	31	217.1	37.64					0.40	0.35
							0.804	0.129	69.06	37.06		
1979	64	29	37	28	243.7	46.44					0.44	0.26
							0.716	0.124	20.20	26.58		
1980	91	29	18	48	194.6	32.22					0.53	0.47
1981	96			47							0.49	
										mean	0.37	0.26

Overall s = 0.766

Life Expectancy = 3.76 years

*see text for explanation of symbols.

The Annual Mortality Estimates.

Despite the large fluctuations in the annual values of the survival rate , s (see Tables 3.21 (males), and 3.22 (females)), the large confidence limits shown in Fig. 3.11 (see also,note on previous page) determined that the overall estimate of s , for both males (0.774) and females (0.766), are a good estimate of the survival rate. There was no significant difference between the sexes, so for both sexes,

$$s = 0.77$$

and the annual mortality (plus emigration) was,

$$(1 - s) = 0.23$$

The Population Size Estimates.

The estimations of the size of the population of the $1.04km^2$ study area are given in Table 3.21 (males), and 3.22 (females), and presented graphically, together with their confidence limits in Fig. 3.12 (see also, the note on the previos page).

In all years the female population was estimated as larger than the males, and this is interpreted as a reflection of the greater dispersal of the females (see Section 3.3.5 , and assuming an equal sex ratio). The male estimate is associated with the $1.04km^2$ study area, but the females can only be associated with a larger, unknown area.

A decline in population was shown by both sexes during the study, and for males this was from 251 in 1975, to 162 in 1980, an apparent decline of 35% in five years.

An overall estimate of population density is $200pairs.km^{-2}$.

Fig. 3.11 The Estimated Annual Survival Of Males And Females.

The estimated values are indicated by horizontal lines, with 95% confidence limits as verticals.

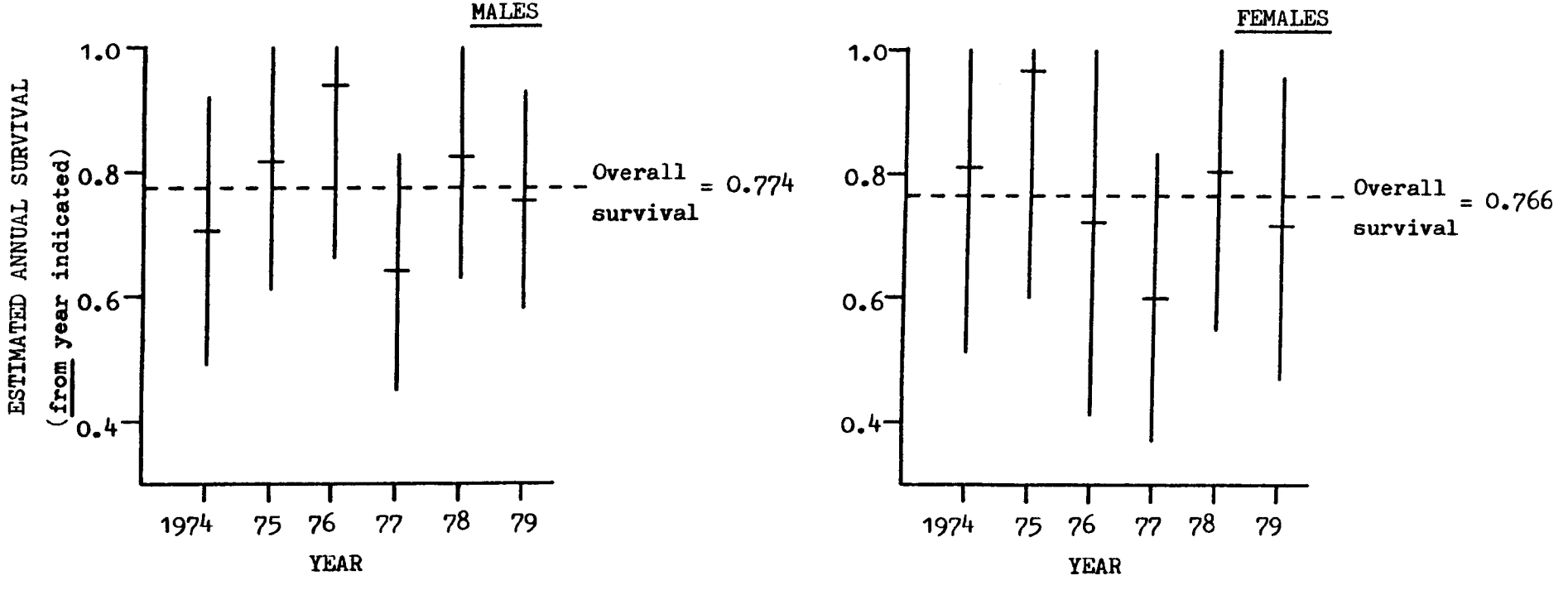
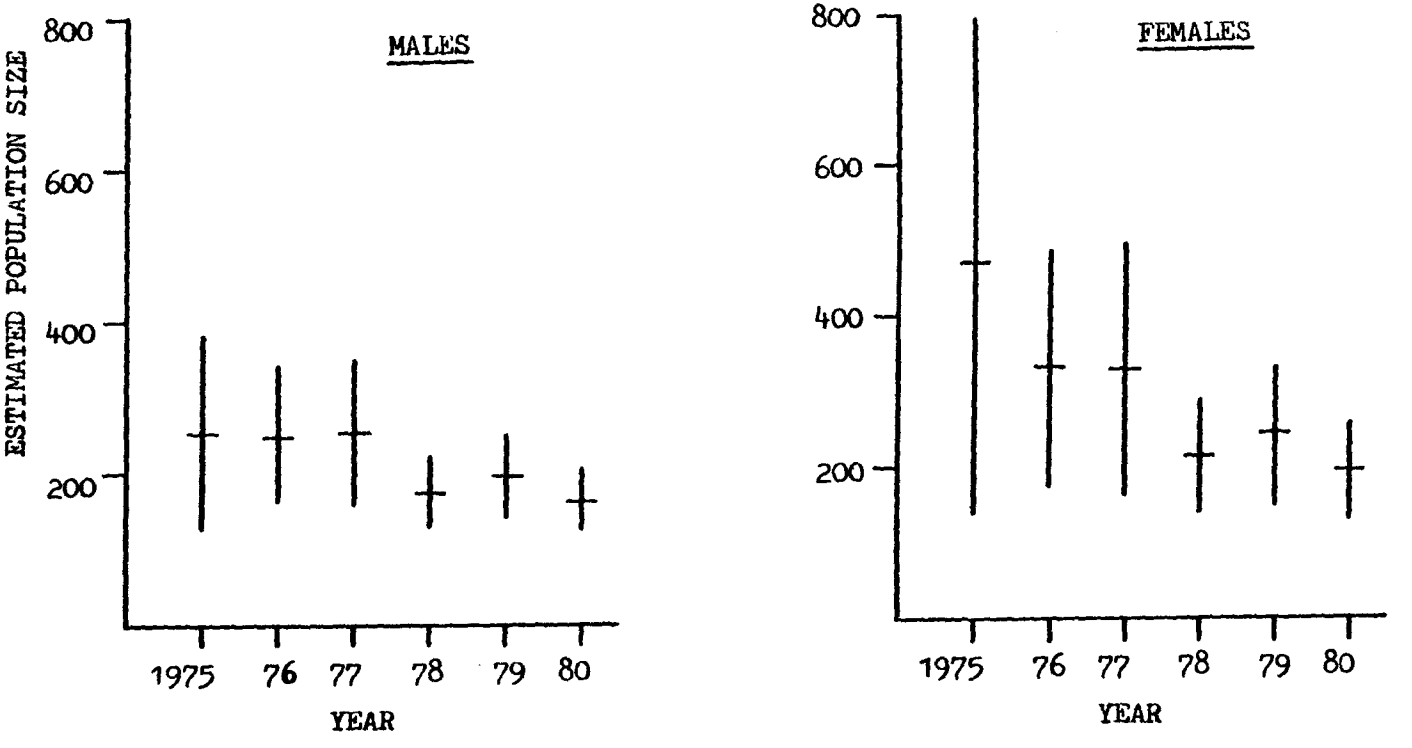


Fig. 3.12 The Estimated Population Size Of Males And Females.

The estimated values are indicated by horizontal lines, with 95% confidence limits as verticals.



3.3.8 The Population Distribution Outside Of The Breeding Season.

Reports of individuals from this breeding population were gained in one of four possible ways. Firstly, the bird was ringed elsewhere before its capture in this study. Secondly, after its capture in this study the bird was controlled elsewhere. Thirdly, thecolour marks were reported such that there was no doubt about the identity of the individual. Lastly, the colour marks were reported such that the individual was not identified, but was definately from this study.

The distribution of reports is summarised in Appendix 5.

From the individuals positively identified the possible influences on the distance moved from the breeding area were investigated. There was no significant correlation between the time (months) from the breeding season (May and June), and distance from the breeding area;

Spearman Rank-Order Correlation Coefficient, $r_s = -0.208$

$P(\text{with } 55 \text{ df.}) > 0.1$

This indicated that migration was not a gradual process, since if it was the reports would have become more distant with time. Therefore, all reports of identified individuals outside the breeding season are used for a further analysis.

The distance from the breeding area was analysed for correlation with the mean values of measurements of the adults taken during the breeding season. The results are given in Table 3.23 , and demonstrate that the distance of the report of a bird was significantly positively correlated with the amount of breeding plumage attained. In addition, there was a related significant negative correlation between the latitude of the report and the breeding plumage. This is presented graphically in Fig 3.12 .

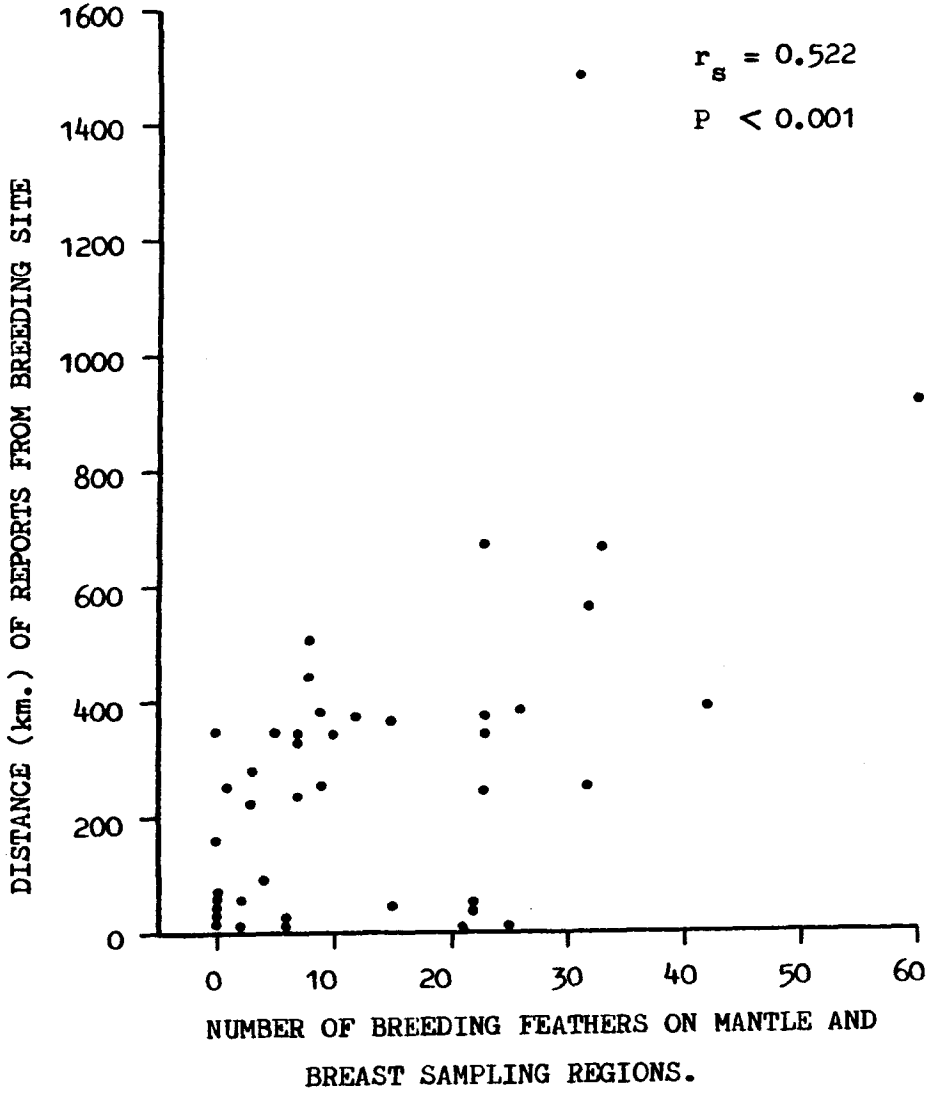
Table 3.23 The Analysis Of The Adult Measurements And Their Place Of Report Outside Of The Breeding Season.

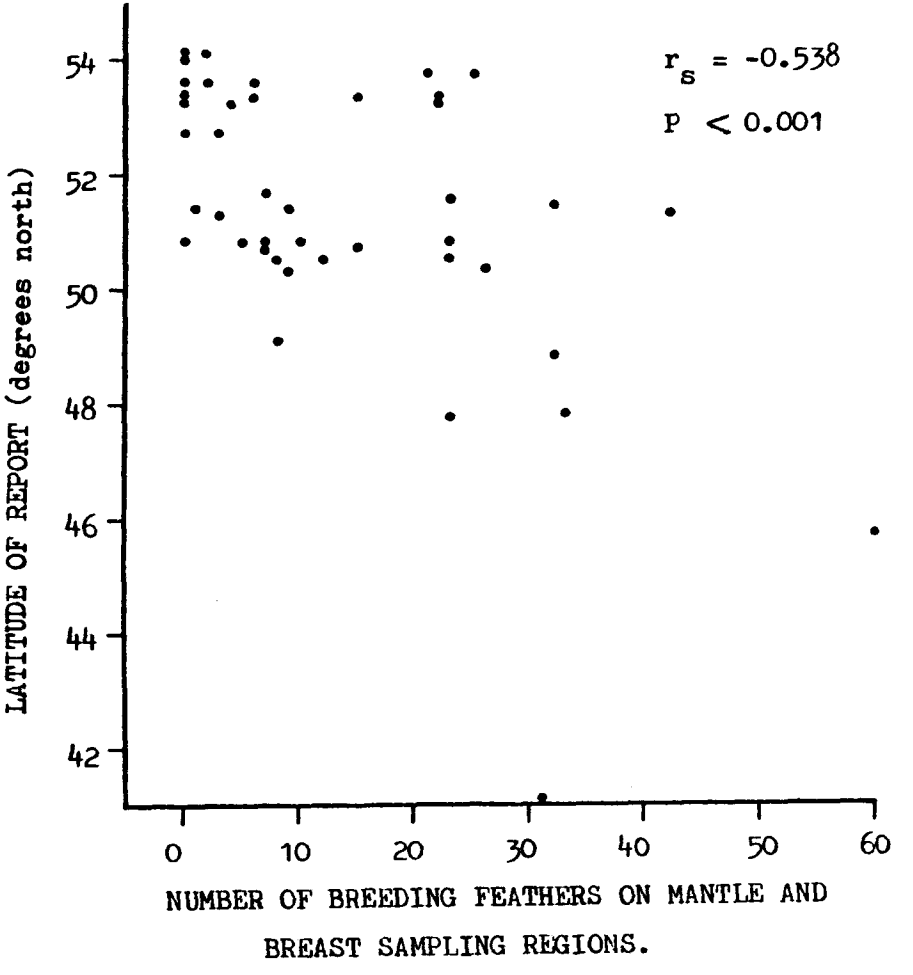
The site of all reports of identified individuals from July to March was compared with their mean measurement. Two aspects of the site of report were used, the distance from the breeding area, and the latitude of the site. The sample size was 42, and the analysis was by the Spearman Rank-Order Correlation method.

Adult parameter		Distance from breeding site.	Latitude of report.
Weight,	r_s	0.246	-0.227
	P	n.s.	n.s.
Wing length,	r_s	0.246	-0.258
	P	n.s.	n.s.
Bill length,	r_s	0.022	-0.036
	P	n.s.	n.s.
Tarsus length,	r_s	0.189	-0.230
	P	n.s.	n.s.
Tarsus width,	r_s	-0.160	0.206
	P	n.s.	n.s.
Breeding plumage attained.			
Mantle,	r_s	0.456	-0.478
	P	< 0.01	< 0.01
Breast,	r_s	0.476	-0.492
	P	< 0.01	< 0.001
Mantle + breast,	r_s	0.522	-0.538
	P	< 0.001	< 0.001

The amount of breeding plumage attained by a bird, and not its body size, was correlated with its reported site outside of the breeding season.

Fig. 3.13 The Relationship Of Adult Breeding Plumage And The Position Of The Non-breeding Site.





3.4 Discussion.

The testing of the assumptions of the Jolly (1965) capture-recapture method indicated that the recapture rates were significantly lower for the birds captured for the first time than for those already captured previously. The older birds (>5 years) also had lower recapture rates, but only a subjective assessment was possible, because of the small sample.

In the Temminck's Stint (Calidris temminckii) Hilden (1978) showed a clear trend of increasing mortality with age, that contradicted many studies (references in Hilden, 1978) which showed an independence of mortality on age, except for an initial higher juvenile loss. Grosskopf (1959) even suggested that Redshank mortality decreased with age, but he only studied his population for a short time and could not determine whether this was due to an increasing nest site fidelity. The present study is the first indication that the '1st year' birds have a reduced nest site fidelity that may account for their low recapture rates.

The classic view of age-independent mortality in birds, as criticised by Botkin and Miller (1974), is becoming outdated by the results of long population studies that clearly show there is an increase in mortality with age. Such studies include the Kittiwake (Rissa tridactyla)studied continuously for 20 years (Coulson and Wooler, 1976) and the Great Tit (Parus major , Webber, 1975). The present study has revealed a similar trend as it has progressed.

Previous estimates of overall annual mortality for adult Redshank fall into two distinct classes. Firstly, those determined by general ringing recoveries over large areas (using the method of Lack, 1951, supplemented by Haldane, 1955), and secondly, by intensive

study of small, discrete populations (using the methods of capture-recapture analysis or the non-return rate). Comparisons of the results of these two main methods show a general difference (see Table 3.24), with the latter method giving lower estimates of mortality, that are generally considered to be more accurate (Soikkeli, 1970 and Grosskopf,1964).

The estimated overall annual survival rate of 0.77 determined that, to remain stable, the population required an annual recruitment of 0.23 (that is, recruitment = mortality). The population (of males) had, however, apparently declined by about 0.35 in five years, that is 0.08 per annum, so the actual recruitment was approximately 0.15 (= 0.23 - 0.08). The proportion of new birds (males) captured towards the end of the study had apparently levelled off at 0.35 (see Table 3.21 , column $\frac{m_i}{n_i}$), but because of the small proportion of the population captured anually (up to 0.59; see Table 3.21 , column $\frac{n_i}{N_i}$), many of these birds were not first time breeders. At best, only 0.43 (= 0.15 + 0.35) of the birds captured for the first time were first time breeders.

Despite the problems of determining an individual's age, and of identifying replacement nests, this investigation has shown that older birds breed earlier in the season than the young. This is common with many waders, for example the Dunlin (Calidris alpina , Soikkeli, 1967) and the Red-necked Phalarope (Phalaropus lobatus , Hilden, 1972), and many other birds.

The young males that did breed early tended to pair with older females than did the young males that bred later in the season. Grosskopf (1970) also found a similar trend with young females. I consider this probably resulted from there being more older mates

Table 3.24 The Estimates Of Annual Mortality Of Adult Redshank.

Estimates from general ringing recoveries.

% annual mortality.	Place.	Authority.
41	Great Britain to 1958	Boyd, 1962.
32	Sweden to 1958	Boyd, 1962.
57	Denmark to 1956	Boyd, 1962.
41	Others to 1953	Boyd, 1962.
44	Germany	Grosskopf, 1964.

Estimates from population studies.

% annual mortality.	Place.	Population	Authority.
18	Amagar, Denmark	Passage migrants	Boyd, 1962.
25	Germany	Breeding birds	Grosskopf, 1964.
23	N.W. England	Breeding birds	This study.

Table 3.25 Mate Fidelity Of Some Waders.

The estimates of mate fidelity are given as the percentage of pairs, still alive, that reunited in the following year.

Mate Fidelity.	Species.	Authority.
58%	Redshank (Tringa totanus)	Grosskopf (1963)
44-82%	Dunlin (Calidris alpina)	Soikkeli (1967)
62%	Western Sandpiper (C. mauri)	Holmes (1972)
42-50%	Stilt Sandpiper (Micropalama himantopus)	Jehl (1973)
71%	Redshank	Present study.

available early in the season, and not that an older mate enabled the young individual to breed earlier, by passing on 'experience', as suggested by Grosskopf (1970).

In the Kittiwake mate faithfulness increases the efficiency of breeding, but there is also an apparent advantage in breaking the pair bond (Coulson, 1966). In the Red-billed Gull Larus novaehollandiae scopulinus pairs with a low fledging success were more likely to change mates than those with a higher success, and half of the changes of mates resulted in the females breeding earlier than in the previous season (Mills, 1973). Coulson (1966) believes "that there may be a degree of incompatability between individuals which result in unsuccessful breeding, and it is clearly an advantage for pairs to split up in the hope that they find a new mate who is more suitable".

In the present study no influence of nesting success on mate fidelity was determined (but this may be a poor indicator of breeding success), and earlier breeding of faithful pairs was not determined by Grosskopf (1970) or in the present study.

Other advantages of mate fidelity can, however, be envisaged, for example, pair maintainence behavour might be reduced to provide more time for feeding and other vital activities, or the probability of nest desertion by just one member of the pair (see Section 3.3.6) might be reduced.

Estimates of mate fidelity for other monogamous waders have been produced that give the percentage of pairs, still alive, that reunited in the following year. These are shown in Table 3.25 , together with the somewhat higher estimate of 71% from this study. This estimate can be interpreted better when combined with the

mortality estimates (see Fig. 3.9), because it gives an overall indication of the fate of pairs in the following year; for example, only 42% of pairs were paired together in the following year.

The probability of remaining faithful for a further year was greater for previously mated pairs than for new pairs, and this resulted in many pairs being faithful for many years.

The high degree of nest site fidelity shown by both sexes, on forming new pairs, determined that pairing probably occured on the breeding ground. The strong site fidelity was also a major factor in the mate fidelity and mate selection, because it limited the 'choice' of mates thus; if males are considered as the 'stationary' sex (that is, the median distance moved between nests, on changing mates was 55m., significantly less than the females' 137m.), then the mobile females did not go very far to find their new mate. Within the area of a radius of the median distance moved by a female on changing mates, that is, roughly 6ha., there would have been, on average, a choice of 12 males (= 200pairs ÷ 104ha. x 6ha.). Further, only a few of these would have been available for pairing at one time, so the 'choice' of mate was restricted to a very few individuals.

This restricted choice would favour mate fidelity and reduce any overall selection of mates (none was found on the basis of size). It would also favour the definite renewed faithfulness, following divorce, that was observed at a very low frequency, thus; if, following a divorce, both members of an original pair were 'looking' for new mates again, one would be amongst the few individuals available to the other for mating. Therefore, renewed faithfulness would be a strong possibility.

The nest site fidelity of the Redshank is very similar to

that of the Dunlin (Soikkeli, 1970b). The movements by males with new mates were the same as those of faithful pairs, but the nest site fidelity of the females with new mates was significantly lower. This same sex bias is common to other species as well; for example, Great Tit (Harvey et al , 1979), Reed Warbler (Acrocephalus scirpaceus , Catchpole, 1972), and Skylark (Alauda arvensis, Delius, 1965).

Population size.

This population of approximately 200pairs.104ha.$^{-1}$, that is, 1.9pairs.ha.$^{-1}$, cannot be directly compared to Grosskopf's (1959) population of approximately 90pairs.18ha.$^{-1}$, that is, 5.0pairs.ha.$^{-1}$, because he concentrated on a very small area of high population. Comparable, selected areas could have been found within the present study area. Clearly demonstrated here is a general rule that density estimates, derived from small areas, must be carefully interpreted for species that show an aggregated distribution.

Distribution outside the breeding season.

This very specific breeding population has shown a widespread distribution outside the breeding season, with most recoveries coming from the coast of Wales, W. England and W. France. Despite the great difficulty in quantifying the distribution, most of the population appears to overwinter in S.W. England.

The high degree of winter site fidelity of many waders (see Hale, 1980, p.127) is also seen for the Redshank in this study (see Appendix 5).

The body size (as estimated by weight, wing, bill and tarsus lenght and tarsus width) was not related to the latitude of the wintering site, which agrees with the inter-population comparison by Hale (1973), but the amount of breeding plumage

attained was correlated with the latitude. Hale (1971) considered the British population to be in a 'hybrid zone', with a characteristic variation in the attainment of a full breeding plumage. This variation has been partly explained in this study by the variation in latitude of the wintering area. Hybridisation may disrupt the pattern of migration which indirectly determines the amount of breeding plumage. This may occur through differences in temperature or photoperiod, but can only be verified by the experimental manipulation of the environment of captive birds.

CHAPTER FOUR - THE EGGS.

4.1 INTRODUCTION.

From the careful measurement of the eggs in numerous clutches two aspects of the size of the eggs are investigated in detail. These are the influence of laying order and maternal size on egg size. In addition, the variation of egg size is considered at three levels; within a clutch, between clutches of a female and of different females.

The weight loss of eggs during incubation is determined and a 'field method' for assessing the stage of incubation of a clutch is described.

The nesting period is measured in two parts, firstly, the period of egg production, the laying period, and secondly, the time from completion of the clutch until its hatching, the incubation period.

Finally, the degree of hatching synchrony within clutches is determined, and the influence of laying order on the hatching order is investigated from the broods observed to hatch asynchronously.

4.2 METHODS.

4.2.1 Processing the Clutch.

When a clutch was found for the first time, the eggs present were marked with a code for egg and nest number, and two measurements were taken from all eggs (see Fig. 4.1).

a) length (l) - the maximum length.

b) width (w) - this was determined by measuring one axis, then rotating the egg through 90 degrees, and measuring again. Two different values were often obtained, due to asymmetry of the egg, and the mean was taken as w.

Both l and w were measured with vernier calipers to 0.02 mm., and enabled the volume of the egg to be estimated (see Section 4.2.2).

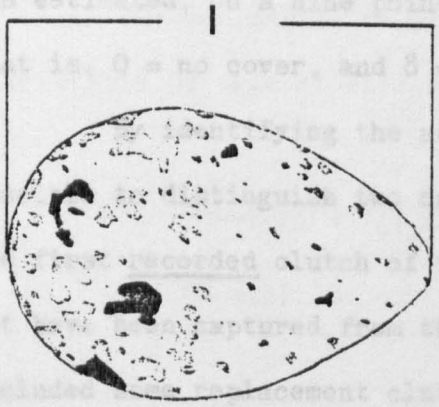
To investigate the changes in density of eggs through incubation, two types of measurement were made, on eggs of known age to provide a standard, against which eggs of unknown age could be aged:

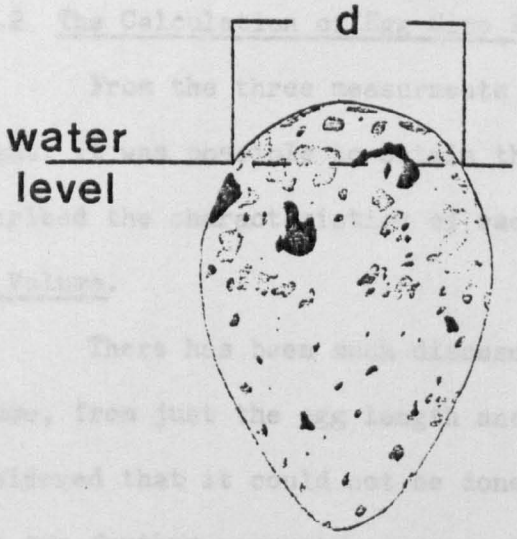
i) Specific gravity was estimated by floating the egg in FRESH water, and measuring either the angle from the horizontal (if it sank), or the diameter of the portion above the level of the water (if floating), see Fig. 4.1.

ii) Egg weight was determined by placing the egg in a nylon bag, and weighing it on a '50 g. Pesola' spring balance, to 0.1 g. Care was taken to allow free movement of the spring, by protecting it from the wind.

The laying order of eggs, within a clutch, was only determined by addition to an already marked , incomplete clutch. The order was not inferred by the degree of soiling, assuming that a dirtier egg was laid earlier.

Fig. 4.1 Egg Measurements.



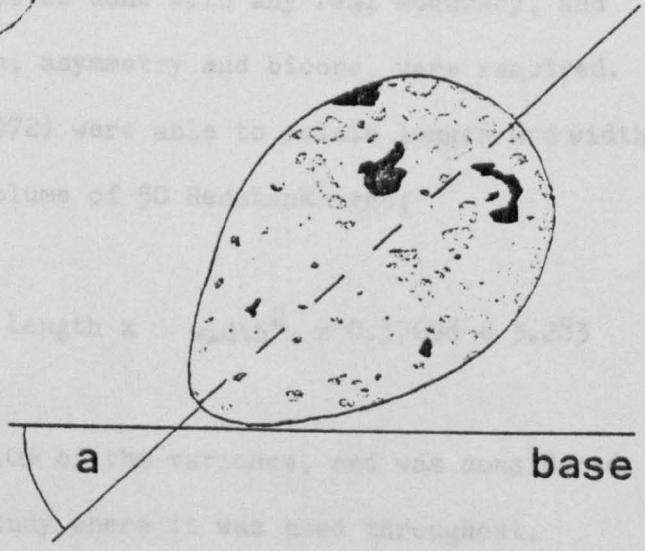


l - Egg length.

w - Egg width.

d - Floating diameter.

a - Flotation angle.



The cover afforded a clutch, by vegetation around the nest, was estimated, on a nine point scale, in a similar way to cloud cover, that is, 0 = no cover, and 8 = total cover.

By identifying the adults, captured at the nest, it was possible to distinguish two catagories of clutch. A first clutch was the first recorded clutch of the year for the pair. The adults may not have been captured from the first nest, and so this catagory included some replacement clutches, especially towards the end of the season. Replacement clutches were definite repeat clutches, since the pair, but more usually just an individual, was previously caught at another nest.

4.2.2 The Calculation of Egg Size Parameters.

From the three measurments of the eggs, length, breadth and weight, it was possible to obtain three other parameters, that further described the characteristics of each egg.

Egg Volume.

There has been much discussion on the estimation of egg volume, from just the egg length and breadth. Preston (1974) considered that it could not be done with any real accuracy, and that two further parameters, asymmetry and bicone, were required. However, Vaisanen et al (1972) were able to relate length and width to the measured internal volume of 50 Redshank eggs;

$$\text{Internal Volume} = \text{Length} \times \text{width}^2 \times 0.37698 + 3.283$$

This explained 88.0% of the variance, and was considered accurate enough for this study, where it was used throughout.

Egg 'Density'.

The estimation of egg 'density' was necessary to relate the weights of eggs of different volumes. It was estimated thus;

$$\text{Egg 'density'} = \frac{\text{total weight}}{\text{estimated internal volume}}$$

and as such was not a true density estimate.

4.3 RESULTS.

4.3.1 The Variation Of Egg Size Between Different Clutches Of The Same Female.

The size of an egg is expressed by several parameters that remain constant throughout the period of incubation. These are the maximum length, maximum width and internal volume. Egg weight is not considered because the weight loss of eggs during incubation (see Section 4.3.5) would restrict the analysis to those clutches found before incubation began.

In some wader species there are differences in egg size between clutches of the same female, both within and between years; for example, the eggs of Temminck Stint's (Calidris temminckii) first clutches were smaller than in the second, and in the Dunlin (C. alpina) there were significant differences between clutches in four years (Vaisanen et al, 1972).

The variation of egg size between first and replacement clutches.

In this study it was unknown, for most clutches, whether they were first or replacement clutches, so initially it is necessary to determine if this factor influences the egg size.

All definite replacement clutches produced by the same pair, and therefore the same female, as a previous clutch are used in a comparison of the mean egg size parameters. This is shown in Fig. 4.2, and analysed in Table 4.1. There is no significant difference between first and replacement clutches of the same pair, with respect to the mean clutch parameters of egg length, width and volume. It is therefore possible to investigate other aspects of egg size without reference to this often unknown factor.

Fig. 4.2 The Comparison Of Mean Egg Size Of First And Replacement Clutches Of The Same Female.

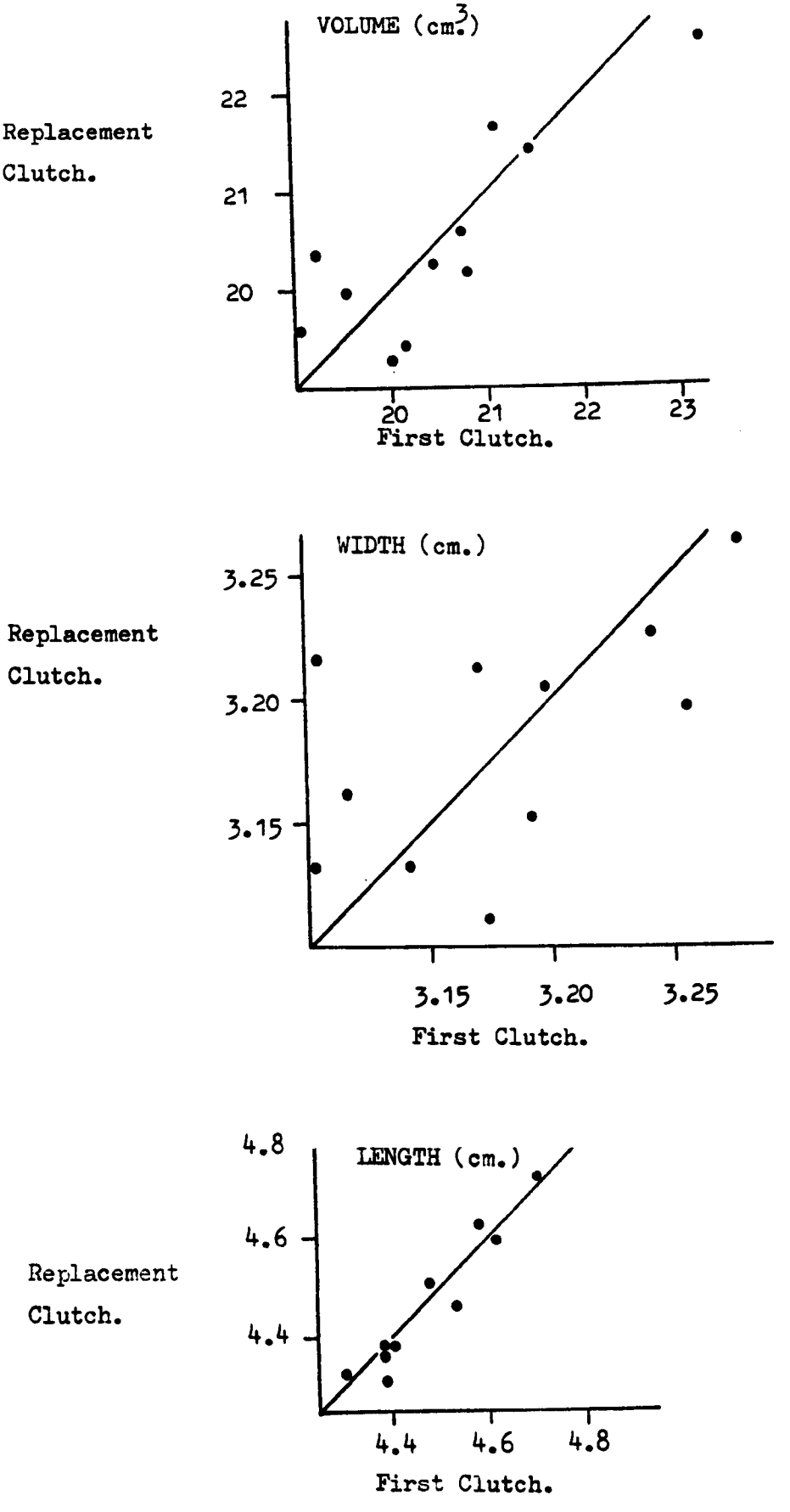


Table 4.1 The Variation Of Mean Egg Size Between First And Replacement Clutches Of The Same Female, In The Same Year.

Paired t-test of the difference, first - replacement clutch.

mean egg size parameter.	Length (cm.)	Width (cm.)	Volume (cm^3)
sample size, n.	11	11	11
mean difference.	0.022	-0.004	0.043
sample variance.	0.003	0.003	0.407
standard error.	0.016	0.016	0.192
t-value.	1.421	0.245	0.222
P(n - 1 d.f.).	n.s.	n.s.	n.s.

There was no significant difference, in all three egg size parameters, between first and replacement clutches.

The variation of egg size between years.

Large differences in egg size between years, would necessitate the transformation of sizes before grouping all years together, to reduce the influence of the years. The differences are investigated by comparing the mean egg size of the clutches produced by the same pair in successive years. Fig. 4.3 gives the data that are analysed in Table 4.2 .

There are no significant differences between the three mean egg size parameters of 1980 and 1981. However, between 1979 and 1980 the mean egg length significantly decreased by, on average, 0.76mm. , and the mean egg width increased by 0.22mm. The volume was not significantly different.

Despite these differences, further investigations are made by combining data from all years, because the observed differences are small.

The constancy of mean egg volume of clutches produced by the same female is used in Section 3.3.2 as a basis for objectively sexing some Redshank.

Fig. 4.3 The Comparison Of Mean Egg Size Of Clutches In Successive Years Of The Same Female.

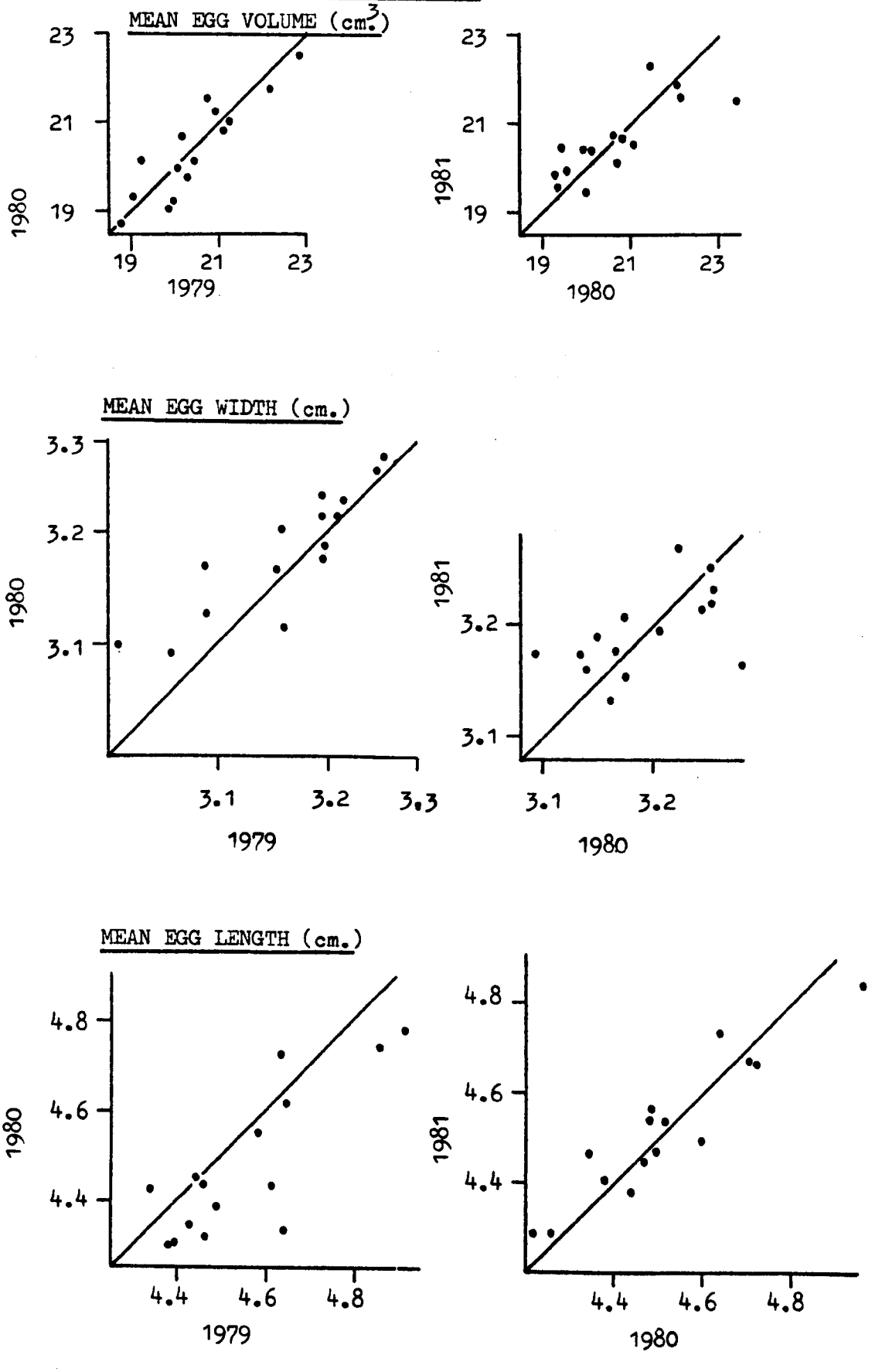


Table 4.2 The Variation Of Mean Egg Size Of Clutches From The Same Female, In Different Years.

Paired t-test of the difference between years.

me

mean egg size parameter.	Length (cm.)	Width (cm.)	Volume (cm^3)
1979 - 1980			
sample size, n.	15	15	15
mean difference.	0.076	-0.022	0.050
sample variance.	0.010	0.001	0.268
standard error.	0.026	0.009	0.134
t-value.	2.921	2.436	0.374
P(n - 1 d.f.)	< 0.02	< 0.05	n.s.
1980 - 1981			
sample size, n.	15	15	15
mean difference.	-0.003	0.000	-0.009
sample variance.	0.005	0.002	0.535
standard error.	0.018	0.012	0.189
t-value.	0.192	0.017	0.049
P(n - 1 d.f.)	n.s.	n.s.	n.s.

From 1979 - 1980 the length had significantly decreased, and the width significantly increased, the net effect being no significant difference in mean egg volume between clutches of the same female. From 1980 - 1981 there was no such significant differences.

4.3.2 The Influence Of Laying Order, Within A Clutch, On Egg Size.

In several wader species, the order in which the eggs were laid, within a clutch, has influenced the size of the individual eggs, for example, Dunlin (Calidris alpina) and Temminck's Stint (C. temminckii) (Vaisanen et al 1972).

During the three years of this study sixty-eight clutches of four eggs were found, in which the laying order of all eggs was known. A two way analysis of variance considers the clutches as 'blocks', and the laying order as 'treatment', see Table 4.3 This is summarised in Table 4.4 by the multiple comparison method of Scheffé (1959), the aposteriori test considered to be most conservative, that is, the one least likely to make a 'Type 1' error of falsely rejecting the null hypothesis (see Steel and Torrie, 1980, p.183).

The last egg of a four egg clutch is significantly narrower than the previous three (which are not different from one another). There is no significant effect of the laying order on egg length, and therefore, the effect on width also results in a significant decrease in the volume of the fourth egg.

Table 4.3 The Two Way Anova Of The Influence Of Laying Order On Egg Size.

EGG WIDTH (cm.)

Source	df	SS	MS	F	P
Clutches	67	1.0099	0.015	10.50	
Order	3	0.1076	0.036	24.97	< 0.001
Error	201	0.2886	0.001		
Total	271	1.4060			

SE of difference = 0.0065

EGG LENGTH (cm.)

Source	df	SS	MS	F	P
Clutches	67	6.7787	0.101	11.40	
Order	3	0.0055	0.002	0.21	> 0.05
Error	201	1.7843	0.009		
Total	271	8.5685			

SE of difference = 0.0162

EGG VOLUME ($cm.^3$)

Source	df	SS	MS	F	P
Clutches	67	248.66	3.71	13.04	
Order	3	12.45	4.15	14.58	< 0.001
Error	201	57.23	0.28		
Total	271	318.34			

SE of difference = 0.092

There is a significant influence of laying order on both egg width and volume, but not on egg length.

Table 4.4 The Multiple Comparison Investigation Of The Influence Of Laying Order On Egg Size, By The Method Of Scheffe (1959).

Egg Width.

For P=0.01 Scheffe's critical value = 0.0219 cm.

Ranked laying order:	4	1	3	2
Mean width (cm.)	3.1612	3.2003	3.2057	3.2123
Eggs not significantly different at P=0.01 are joined by a line.				

Egg Volume.

For P=0.01 Scheffe's critical value = 0.31 $cm.^3$

Ranked laying order:	4	1	3	2
Mean volume ($cm.^3$)	20.40	20.84	20.88	20.93
Eggs not significantly different at P=0.01 are joined by a line.				

Egg Length.

The analysis of variance (Table 4.3) indicated no significant effect of laying order on egg length.

The last egg to be laid, of a four egg clutch, was significantly narrower than the previous three (which were not different from one another). There was no significant effect of laying order on the egg length, and therefore, the effect on the width also resulted in a significant decrease in the volume of the fourth egg.

4.3.3 The Components Of The Population Variation Of Egg Volume.

It was shown, in Section 4.3.1 , that egg volume was the most consistent mean egg size parameter of clutches of each female, between years and within years. The variation in egg volume was considered at three levels in the population; between eggs of a clutch, between clutches of a female, and between clutches of different females, using the method of heirarchical analysis of variance with unequal replicates (see Sokal and Rohlf, 1969, p.274). Only clutches produced by the same pair were considered (to ensure the same female), and the results are given in Table 4.5.

The only significant variance component of egg volume was between females, which represented 43.6% of the total variance. The remainder of the total variation was attributable to the variation within a clutch (56.4%) which probably resulted from the significantly smaller volume of the last laid egg (see Section 4.3.2). The variation between clutches of the same female was extremely small and provides further evidence for the method of sexing described in Section 3.3.2, the 'M.E.V. method'.

Table 4.5 The Components Of The Population Variation Of Egg Volume.

The volumes of eggs of clutches produced by known females were used to consider the variation of eggs within the population at three levels:

Source	df.	SS	MS	F	Expected MS
Among females.	42	326.15	7.77	10.64	$s^2 + 3.95s^2_{B<A} + 8.32s^2_A$
Among clutches within females.	48	35.06	0.73	0.67	$s^2 + 3.92s^2_{B<A}$
Among eggs within clutches.	267	292.32	1.10		s^2
Total.	357	653.53			

The coefficients of the mean squares (that is, 3.95 and 3.92) are so similar that it was considered not necessary to adjust the tests of significance.

The only significant variance component of egg volume was between females ($F = 10.64$, $P < 0.005$).

The variance components of egg volume expressed as percentages.

s^2(among eggs within clutches) = 1.10

$s^2_{B<A}$ (among clutches within females) $= \frac{0.73 - 1.10}{3.92} = -0.09 \Rightarrow 0$

s^2_A (among females) $= \frac{7.77 - 1.10 - (3.95 \times -0.09)}{8.32} = 0.85$

Total variance $= s^2 + s^2_{B\ A} + s^2_A = 1.95$

Therefore, $s^2 = \frac{1.10}{1.95} \times 100\% = 56.4\%$

$s^2_{B<A} = \frac{-0.09}{1.95} \times 100\% \Rightarrow 0\%$

$s^2_A = \frac{0.85}{1.95} \times 100\% = 43.6\%$

4.3.4 The Influence Of Female Size On The Mean Egg Size Of A Clutch.

The variation of mean egg volume of the clutches produced by the same female has been demonstrated to be small in relation to the variation between females. This latter source of variation is investigated with respect to the size of the females (only those sexed by the M.E.V. method) by comparison with the measurements of the clutch, and the female at her last capture, see Table 4.6 .

The mean egg width is not significantly correlated with female size, but the mean egg parameters of volume and length are significantly positively correlated with female wing, bill and tarsus lengths. However, the coefficients of determination (r^2) of these significant relationships is less than 0.12, such that only a small proportion of the total variation of egg measurements is explained by the female measurements.

Table 4.6 The Correlation Analysis Of Adult Size And Egg Size.

Adult size parameter	Mean egg size parameter		
	Volume	Width	Length
FEMALE			
Weight	0.23	0.11	0.27*
Wing length	0.33**	0.20	0.33**
Bill length	0.35**	0.20	0.34**
Tarsus length	0.32**	0.19	0.32**
Tarsus width	0.18	0.16	0.12
MALE			
Weight	- 0.03	- 0.09	0.06
Wing length	- 0.05	- 0.01	- 0.07
Bill length	0.01	0.01	0.01

N = 58

P (0.05) = *

P (0.02) = **

P (0.01) = ***

4.3.5 The Weight Loss Of Eggs During Incubation.

The decrease in density of eggs during incubation is mainly due to the loss of water, and it is nearly constant from day to day (for review, see Drent, 1973.). This therefore provides a means of ageing eggs in terms of days of incubation, which is an important addition to this study of breeding biology.

All the eggs weighed before they had recieved a maximum of one day of incubation, provide a weight and density of the 'fresh egg', see Table 4.7.

From the weights during incubation of the eggs that subsequently hatched, the change in 'density' of eggs, with reference to the date of hatching is investigated (Section 4.2.2 explained that the density was calculated from the internal volume and total weight). Fig. 4.4 shows the change in 'density' with time. The rate of change of density shows two phases, firstly, a slow decrease of $0.0049 g.cm.^{-3} day^{-1}$ from 26 to 5 days before hatching, and , secondly, a more rapid decrease until hatching of $0.0187 g.cm.^{-3} day^{-1}$. This later, faster decrease in density corresponds with the breakdown of the membranes and shell of the egg by the pullus, prior to hatching.

In Table 4.7 the weight loss during incubation is determined and overall this represents 17.8% of the fresh weight of the egg.

Fig. 4.4 could provide a means of ageing eggs, but it requires very careful measurement and calculation. A more rapid method, appropiate to the field situation, is to estimate egg density by floating the egg in fresh water, and recording the degree of flotation.

Fig. 4.5 shows the 'standard' produced from measurements of eggs of known age. Despite the great variation of flotation of eggs of a single age, the method provides a rapid, approximate answer, to the important question of when a clutch was laid, and when it will hatch.

Fig. 4.4 The Decline Of Egg Density During Incubation.

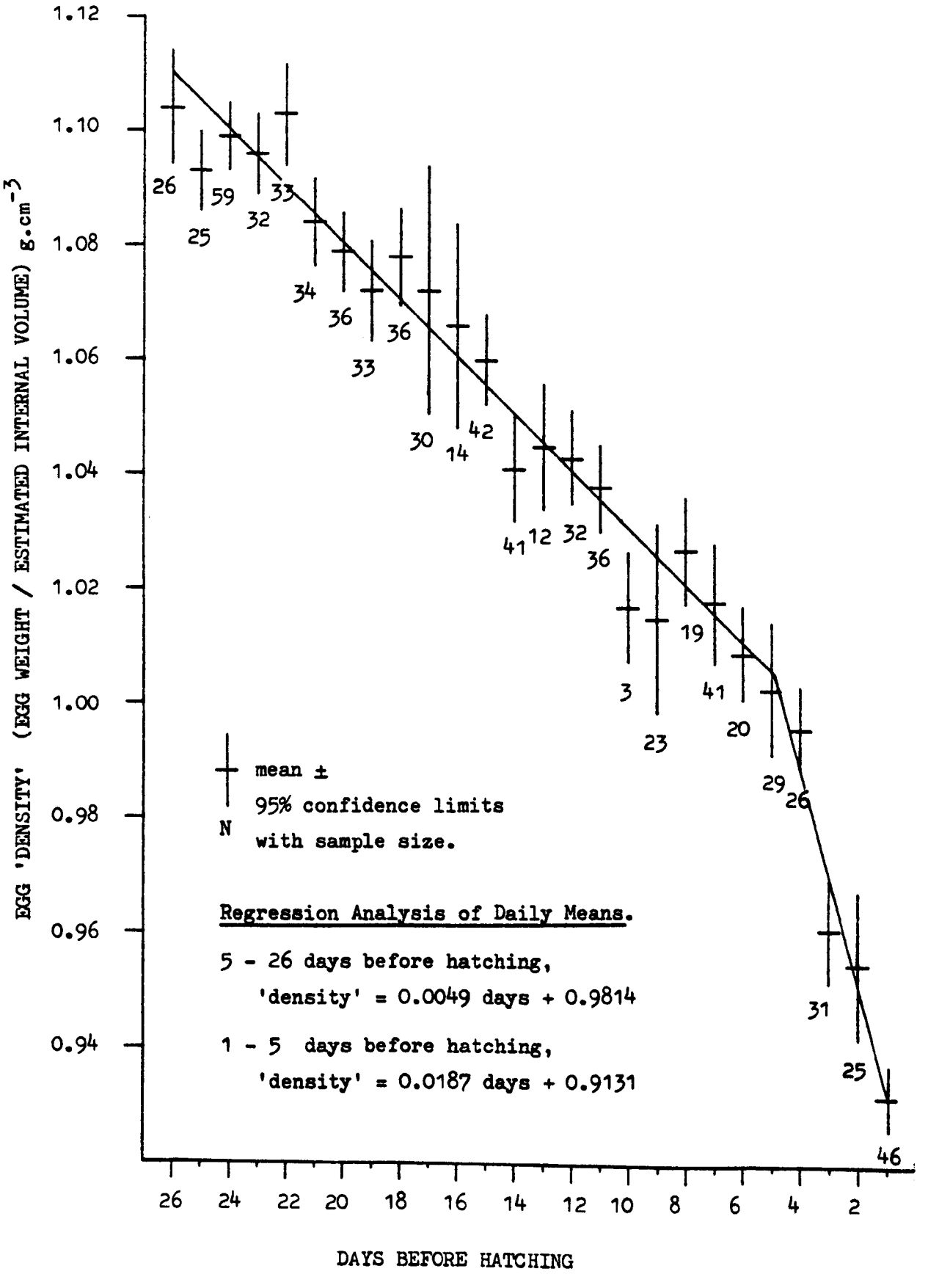


Table 4.7 The Description Of The Mean Fresh Egg And Its Weight Loss During Incubation.

381 eggs were weighed before they had recieved a maximum of one day of incubation, and these were considered as "fresh weights".

	fresh weight	estimated internal volume	density
mean	22.94 g.	20.58 $cm.^3$	1.114 $g.cm.^{-3}$
95% confidence limits	± 0.37	± 0.11	± 0.002

*1 = see Fig. 4.4

For 5 - 26 days before hatching*1;

decrease in density = 0.0049 $g.cm.^{-3}day^{-1}$

weight of egg of mean volume = 0.0049 x 20.58

= 0.101 $g.day^{-1}$

For 1 - 5 days before hatching*1;

decrease in density = 0.0187 $g.cm.^{-3}day^{-1}$

weight of egg of mean volume = 0.0187 x 20.58

= 0.385 $g.day^{-1}$

During the incubation period of 26 days;

weight loss = 20.58((0.0049 x 21) + (0.0187 x 5))

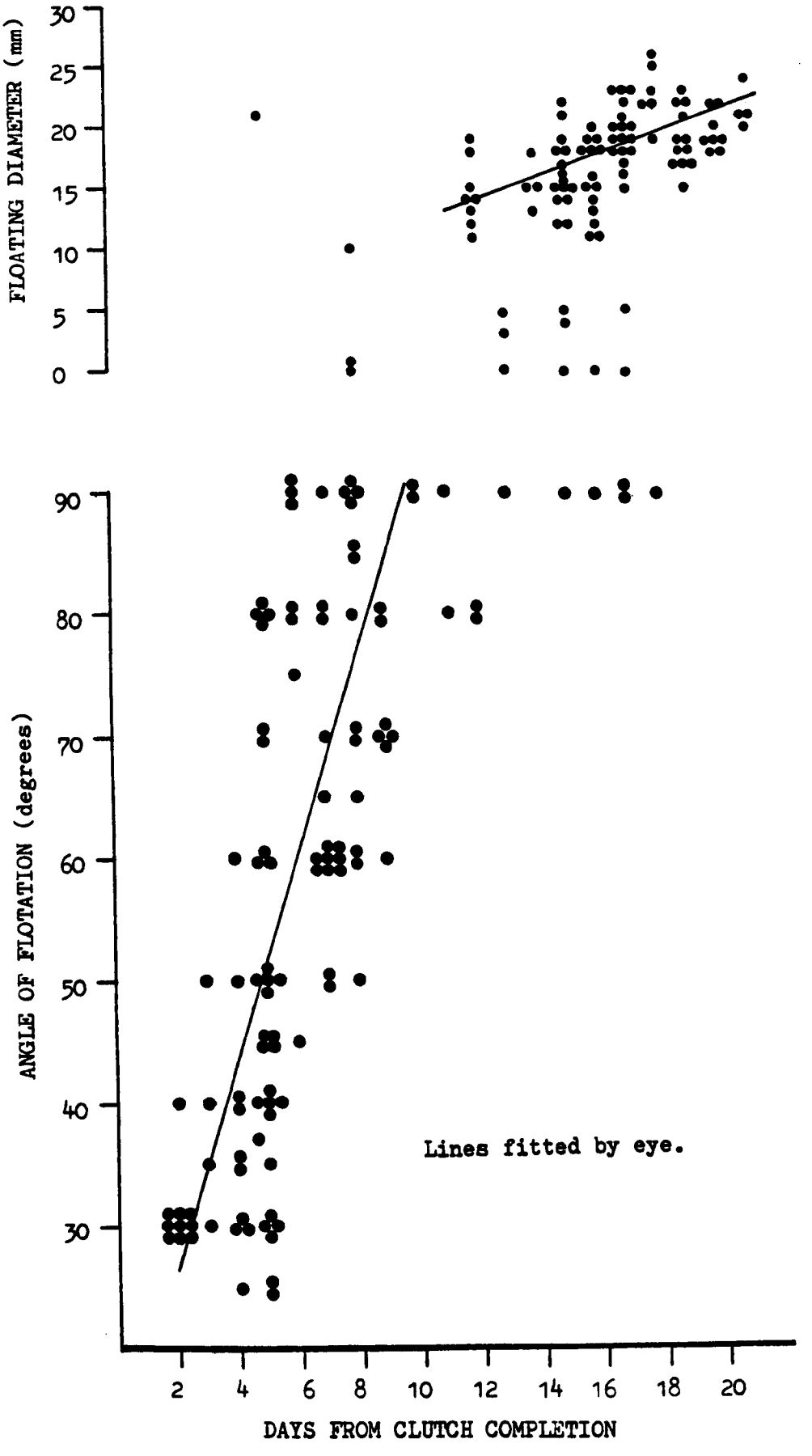
= 4.08 g.

The percentage of the fresh weight lost during incubation

$$= \frac{4.08}{22.94} \times 100\%$$

= 17.8%

Fig. 4.5 The Flotation Standard For Eggs.



4.3.6 The Clutch Size.

The Redshank is a determinate layer, almost exclusively producing clutches of four eggs. However, the determination of the frequency of deviation from this normal clutch size is very difficult, since the loss of individual eggs was quite common (both during and after clutch completion), and occasionally a single egg (and once, two) was laid in another nearby nest scrape. Occasionally extra single eggs (of similar dimension and patterning to the clutch) appeared during incubation, and in one nest three eggs were added, singly, after about fifteen days of incubation.

The assumption that all clutches were composed of four eggs would be very close to reality, so this is used throughout this study.

4.3.7 The Laying Period.

The period from the first to the last egg of a clutch is important in considering nest losses, since it represents a period of risk in addition to the incubation period. It is also useful, in some cases, in estimating the date of clutch completion.

The clutch is made up to its maximum size by the addition of single eggs at discrete intervals. These are investigated by measuring the interval between eggs (to the nearest half day) of all clutches first discovered with only one egg, and intensively observed, by at least daily visits, until the production of the fourth egg.

Table 4.8 shows the laying period to last for 4.5 days, with the interval between eggs of approximately 36hrs.

Table 4.8 The Intervals Between Egg Laying, Within Clutches.

Interval	Sample size.	Mean (days).	Standard error.
Egg 1 - Egg 2	58	1.60	0.216
Egg 1 - Egg 3	58	3.10	0.091
Egg 1 - Egg 4	60	4.49	0.185

Therefore;

Egg 1 - Egg 2 = 1.60 days = 38.4 hrs.

Egg 2 - Egg 3 = 1.50 days = 36.2 hrs.

Egg 3 - Egg 4 = 1.39 days = 33.4 hrs.

Table 4.9 The Observed Incubation Periods, 1979 to 1981.

Incubation length (days).	1979	1980	1981	Total
24	7	2	1	10
25	8	4	13	25
26	8	15	17	40
27	4	5	6	15
28		4	1	5
29		1		1
30		1		1
32		1		1
Sample size.	27	33	38	98
Mean.	25.33	26.55	25.82	25.93
Standard error.	0.20	0.28	0.14	0.13

4.3.8 The Length Of The Incubation Period.

It is necessary to determine the time from the completion of the clutch to the hatching of the first egg (that is, the incubation period) for several reasons. Firstly, this period, together with the time to complete the clutch (see before), is when the investment of the adults in breeding is at risk from the many sources that were investigated in Section 2.3.4 . Secondly, to efficiently ring and measure the pulli (in the nest), of clutches of known (or estimated) date of clutch completion, this period and its variation had to be known.

Although some nests showed incubation commencing before clutch completion (by the clutch feeling warm to the touch), it is not known to what extent this occured in the population (because it was difficult to objectively determine). Therefore, the period estimated is from the laying of the last egg, to the hatching of the first pullus. It is calculated, in Fig. 4.9 only from those nests in which the timing of both these events was known to within one day.

The slight variation between years is not explained, and the approximation of 26 days is considered a good overall estimate of the incubation period.

4.3.9 The Influence Of Laying Order On Hatching Order.

Several studies have revealed some association between the laying and hatching orders, and Miller (1979) considered this the general rule in waders. The most frequently known egg order was for the last laid, and the present study indicated that incubation began in some nests before this last egg was laid. Therefore, the order of hatching of the last egg laid in clutches of four that all hatched successfully, is investigated in Table 4.10 .

Only fifteen broods of four pulli were observed in which the order of hatching of the fourth egg was known. 40% of clutches hatched apparently synchronusly, but when asynchronus hatching occured there was a distinct trend towards the fourth egg hatching later in the brood order.

Table 4.10 The Influence Of Laying Order On Hatching Order.

Fifteen broods of four pulli were observed in which the order of hatching of the fourth egg was known.

Where the pullus from the fourth egg may have hatched in up to three 'orders', it's value (one) is divided by the order, thus;

if the fourth egg could have hatched in the order, 1st or 2nd , these are each given a half value.

Order of the fourth egg hatching.	Observed frequency.	Expected frequency (if no trend).
1st	1.33	2.25
2nd	1.83	2.25
3rd	2.50	2.25
4th	3.33	2.25
Total	9.00	9.00

Because of the small sample no significance can be attached to this result, but the trend is clearly for the fourth egg to hatch later in the brood order.

6 (40%) broods hatched apparently synchronously, but this value is obviously dependent upon how soon after hatching began within the clutch, that a visit was made to the nest

4.4 Discussion

The mean egg size of this population (estimated internal volume 20.6cm^3 , with a fresh weight 22.9g.) is the largest so far reported for the Redshank, and it extends the trend determined by Vaisanen (1977). This was a general decrease in egg volume eastwards across Europe, with some further decrease southwards, which was interpreted by him as an increase in egg size due to an increasingly maritime climate.

The mean female size of the different populations in Europe was not correlated with the mean egg size (wing length from Hale, 1971, and egg volume from Vaisanen, 1977, $r = 0.518$, $n = 13$, $P > 0.05$) which contrasts with the result found within this population. However, it may be that environmental factors confuse the interpopulation comparison. Also, in contrast with the above result, the Ringed Plover (Charadrius hiaticula) showed an extremely high positive correlation between the regional mean values of wing length and egg size (Vaisanen, 1969, Fig. 7), but in this species there is a much lower variation of breeding habitat, when compared with the Redshank.

The egg size of a determinate layer should be maximised to favour survival of the pulli (see Section 5.4), but the investment is usually limited by food availability. Therefore, a comparison of the mean egg size will partly reflect the quality of the food environment. This was demonstrated in Lapwing (Vanellus vanellus) where the mean egg weight was 8.4% greater on farmland (with abundant food) than on heathland (with sparse, variable food, Murton and Westwood, 1974).

During the non-breeding season Redshank are almost exclusively coastal, feeding on Corophium spp. In the breeding

season some nest at coastal sites, while many become inland feeders. On the Ribble estuary the biomass of Corophium spp. remains high during the spring (6g-dry weight.m^{-2}, Greenhalgh, 1975), enabling migrant waders to lay down fat stores and the breeding Redshank to produce large eggs.

The results of Vaisanen (1977) therefore, may not have indicated an overall eastward decline of egg size, with decreasing maritime influence, but just the decreasing proportion of clutches produced at coastal sites within his different samples.

If, as suggested above, this population is producing eggs of maximum size because of abundant food, it is not too surprising that the egg volume did not vary between years, or between first and replacement clutches. In other populations, where food is more limited, and variable, it may not be so.

In two waders, Little Ringed Plover (Charadrius dubius) and Lapwing, seasonal declines in egg volume were noted (Vaisanen, 1977, p.22) and in another, Temminck's Stint (Calidris temminckii) the volume increased in second clutches (Vaisanen et al, 1972). In the Ruff (Philomachus pugnax) the egg size decreased after 2-4 years of breeding (Andersen, 1951).

In comparison with this study and most other waders, the gulls differ greatly(see Vaisanen et al, 1972, p.40 and references therein), with egg dimensions of a female varying greatly in replacement clutches during the same breeding season and from year to year.

The effect of laying order on the egg size within the order of Charadriiformes, is well established for many Larid species (Vaisanen et al, 1972, p. 38), with the third (last) egg averaging 4.4% smaller than the mean clutch volume. In four wader

species Vaisanen et al (1972) determined the following influences of laying order on egg volume: Temminck's Stint showed an increase in egg volume from the first to the last egg, with the largest difference from the clutch mean of 1.5%. Ringed Plover, Dunlin (Calidris alpina) and Red-necked Phalarope (Phalaropus lobatus) showed no difference between the fourth egg and the rest of the clutch. For the Least Sandpiper (Calidris minutilla), Miller (1979) also found no difference in egg volume with laying sequence.

In contrast to the above, Miller (1979, p.15) stated that, "ordering of egg size, such that large eggs are laid last, is widespread in shorebirds", but he failed to substantiate adequately this claim with examples.

The opposite trend was clearly demonstrated for the Redshank in this study, with a reduction in volume of the last laid egg (by 1.8% of the clutch mean) that was shown to be due to the decrease in the egg width.

Miller (1979) suggested that in waders there are two factors limiting the differential investment (as estimated by size) in eggs according to laying order. These are the lower heat loss from a clutch of similar sized pyriform eggs (see also Andersson, 1978, p. 108), and the hatching synchrony of a clutch where incubation begins at the same time for each egg. The present study has, however, indicated that some incubation began before the last egg was laid (see Section 4.3.8, which is in agreement with Grosskopf, 1958, but Ashcroft (1978) considered it to affect only 11% of nests) The pullus from the last egg would, therefore, be at a disadvantage because its co-ordination would be less than that of the rest of the brood when these are ready to leave the nest.

Where asynchrony of hatching was observed in the present study the last laid egg tended to hatch later than the other three eggs. This pattern of hatching was considered the general trend by Miller (1979), but exceptions are common (for example, Parmalee et al , 1968, and Parmalee, 1970) and interpretation of the degree of asynchrony is questionable and depenedent upon the frequency of observation and the sample size.

Theoretically, the last egg, because of its smaller volume, would require a shorter incubation period than the rest of the clutch. This follows from the interspecific trend described by Rahn and Ar (1974, Incubation(days) = 12.03 x Weight(g.)$^{0.217}$) but the difference in mean volume would only account for a three hour shorter incubation for the fourth egg, compared with the other three.

It does not seem likely, therefore, that the smaller fourth egg has a great influence on promoting synchronus hatching. The narrower last egg may just result from a reduction of the physiological processes of egg formation and laying (Paludan, 1952, and Kendeigh et al , 1956, also suggested this). In this population that is laying very large eggs, such a changing physiology may produce the observed significant effect on egg width and volume of the last egg.

CHAPTER FIVE - THE PULLI.

5.1 Introduction.

A large number of pulli was measured on the day of hatching, and from these the relationship of egg and maternal size to pullus size is investigated. This large sample of pulli also resulted in a few individuals of known age being recaptured throughout the pre-fledging period. These formed the basis of a description of the growth and development of pulli, which also permit an ageing of pulli which had not been marked at hatching.

The development of juvenile plumage and the movements made by broods across the marsh are also considered.

The estimation of mortality factors is not possible because of the extreme elusiveness and mobility of the pulli, but a method is developed to determine this important aspect of the population dynamics of this species in future.

5.2 METHODS

5.2.1 Processing, and Marking the Pulli.

The pulli stayed in the nest for only a short period after hatching, and therefore, to mark them efficiently, it was necessary to predict, with reasonable accuracy, the date of hatching. With visits to each nest, usually, once every two days, and at a maximum interval of three days, careful observation of the eggs indicated the timing of hatching. 'Starring' and 'chipping' commenced two days before the day of hatching, in most cases.

Hatching of a brood was most usually synchronus, but if not it was often possible to allocate a pullus to a particular egg.

Each pullus was fitted with a numbered, metal ring, below the intertarsal joint, and in most cases it could not be slipped off, and lost. In some cases, where the pullus was very small, the metal ring could be slipped off, and to these a numbered, plastic ring of slightly smaller internal diameter was fitted to the other leg. This ensured individual identification on recapture, when a new metal ring could be fitted, if necessary.

The following measurements were then taken;

a) bill length - the distance from the tip of the bill, to the hind margin of the nares, was measured with vernier calipers, to 0.1 mm. This distance was chosen, in preference to others (for example tip to feathers) because it was well defined, enabling each measure to be reliable, and quick to obtain.

b) tarsus length - the distance from the notch on the back of the intertarsal joint, to the lower edge of the last complete scale before the toes diverged, was measured to 0.1 mm. with vernier calipers.

c) weight - as for the eggs (see Section 4.2.1).

The prescence or abscence of an egg-tooth, and whether the downy feathering was dry, or still wet from hatching, were also noted, together with the time and date of measurement.

While processing the brood at a nest, speed was essential to minimise disturbance, and heat loss. The brood was placed in a cotton bag, each pullus was individually processed, and then placed in a separate bag. On completion, the brood was returned to the nest and covered with vegetation. After our hasty retreat, the parent bird(s) quickly returned to brood.

5.2.2 Capturing the Pulli Away from the Nest.

The most difficult, and frustrating aspect of this study was in attempting to capture the pulli away from the nest. This was necessary in order to invetigate their development, and movements, which were only poorly known before.

For a few days after hatching the parents stayed very close to the pulli, which usually remained on the 'surface' of the saltmarsh. These could be fairly easily pinpointed by direct observation, to an area of, perhaps, a square metre. However, as soon as danger threatened, the parental 'alarm call' immediately caused the pulli to seek a hiding place, and 'freeze', making themselves invisible to all but the closest of searches.

As they got older the pulli became more independent of their parents, requiring less brooding, and spent most of their time in the channels of the saltmarsh. They also appeared (!) to become more proficient at hiding, that is, they were more difficult to locate. It cannot be stressed too greatly how difficult the older pulli were to capture, and the time involved per capture was

probably many hours. Further to this, there was no guarantee that a particular pullus would be ringed already, and without, there was little value in the data collected.

The method of capture required two people, one to sight and pinpoint the pullus, and the other to rush at it, making it 'freeze' in a suitable, open site. In ungrazed vegetation a hide was used to make observations at a distance of 20 to 80 m. (dependent upon the adult temperament), while in grazed areas observations were made up to distances of approximately 400 m.

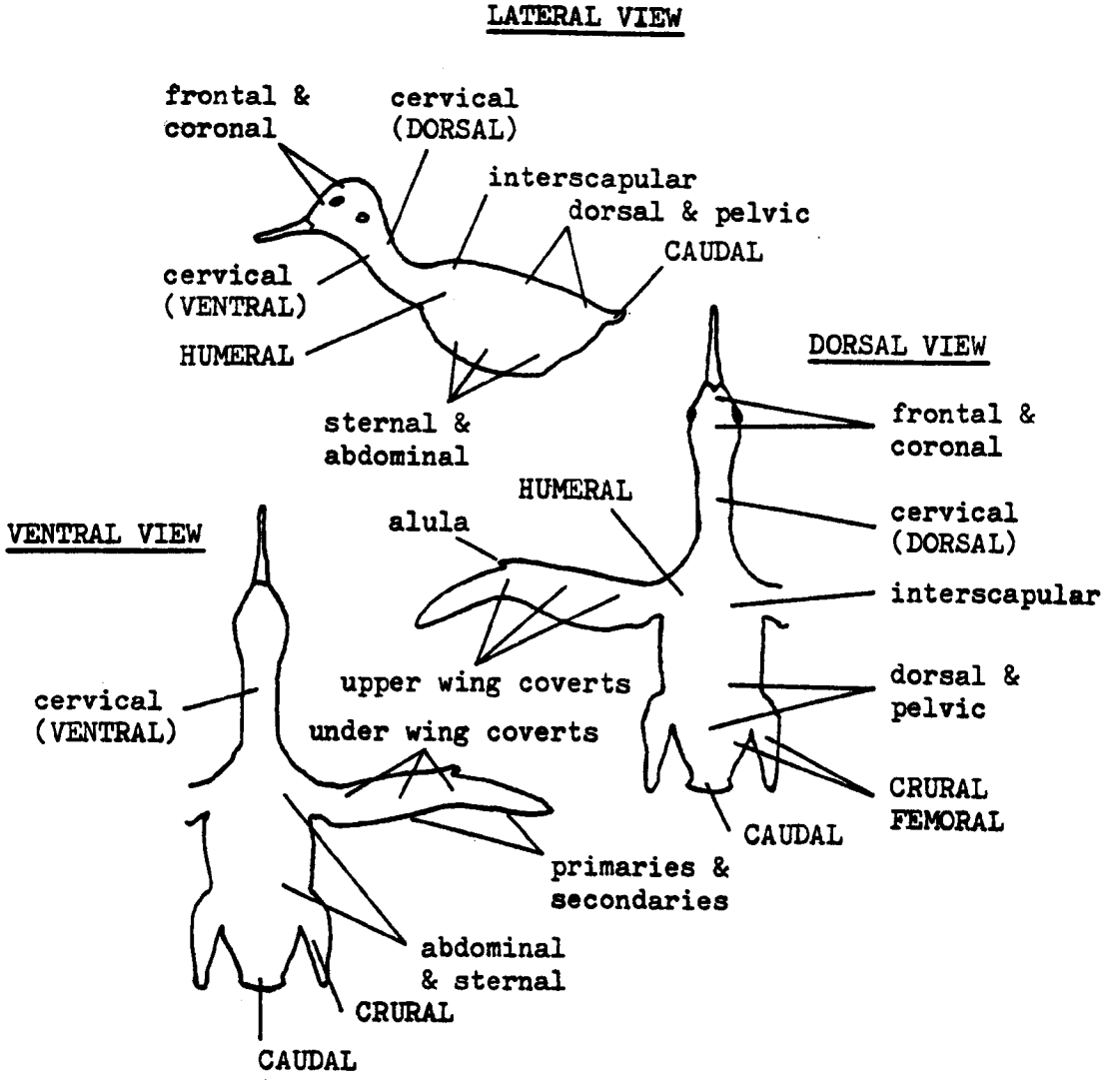
Following a capture, the measurements of Section 5.2.1 were repeated, and the ring number, date, time and position on the saltmarsh noted. In addition, any pullus showing development of the juvenile plumage was subjected to a detailed survey of the feather regions and tracts. This was based on the pterylography described by Holmes (1966b) for the Dunlin (Calidris alpina), a species also in the Family Scolopacidae.

The feather regions and tracts are shown in Fig. 5.1 . For each pullus every feather region was given a 'moult score' relating to the most common stage of feather development within it. The scoring was as follows;

moult score	feather development
0	old (downy) feather
1	still in 'pin' (within waxy sheath)
2	less than $\frac{1}{3}$ full length
3	intermediate length
4	more than $\frac{2}{3}$ full length - waxy sheath present
5	full length - no waxy sheath

Fig. 5.1 The Pterylography Of The Redshank (after Holmes, 1966b).

Feather tracts are indicated by capital letters, and feather regions, within tracts, by lower case letters.



After processing, some individuals were persuaded to hide in vegetation, but if they preferred to run away, care was taken to conceal them, to some extent, in a channel, and allow the parents to return as quickly as possible.

5.3 RESULTS.

5.3.1 The Size Of Pulli In The Nest.

After hatching, the pulli remain within the nest for a period of up to approximately one day. During this period there is, presumably, little environmental influence on pullus development, and this is important in two respects. Firstly, it provides a base level for possible comparison with other populations, and, secondly, it reduces the variation between individuals, and, therefore, enhances the possibility of determining influences on pullus size. Such influences considered in this section are egg and maternal size.

All the pulli measured for the first time while in the nest, that is, 0 days old, are divided into three 'age' catagories;

stage 1 - all downy feathering still wet from hatching.

stage 2 - some downy feathering still wet from hatching.

stage 3 - all downy feathering dry and fluffy.

limited observations suggested that these stages lasted for the following approximate periods;

stage 1 - 0 to 30 mins. after hatching.

stage 2 - 30 mins. to 2 hrs. after hatching.

stage 3 - 2 hrs. to 1 day after hatching.

Table 5.1 shows the mean size of these three catagories, and the comparison of adjacent stages. The pulli of stages 1 and 2 are not significantly different from each other, but are significantly different to those of stage 3. That is, the pulli found to be fully dry from hatching are significantly lighter (weight), with greater bill and tarsus lengths, than the pulli only recently hatched.

Following from this, the size at hatching is only considered for pulli of stages 1 and 2, and this is summarised in Table 5.2.

Table 5.1 The Size Of Pulli Measured When Still Within The Nest.

The pulli were divided into the following stages of development, and are analysed separately;

Stage 1 - all downy feathering still wet from hatching.

Stage 2 - some downy feathering still wet from hatching.

Stage 3 - all downy feathering dry and fluffy.

Pullus stage.		1	2	3
Bill length (mm.)				
mean,	$\bar{x}$	10.839	10.971	11.105
sample size,	N	46	134	247
standard dev.,	S	0.4224	0.4594	0.4611
Tarsus length (mm.)				
	$\bar{x}$	26.575	26.917	27.293
	N	44	134	239
	S	1.2284	0.9710	1.1867
Weight (g.)				
	$\bar{x}$	16.489	16.437	15.851
	N	46	134	247
	S	1.299	1.237	1.210

The comparison of adjacent stages to determine significant differences.

Comparison	Stages 1 & 2		Stages 2 & 3	
	d	P	d	P
Bill length	1.79	n.s.	2.72	<0.01
Weight	0.24	n.s.	4.45	<0.001
Tarsus len.	1.68	n.s.	3.31	<0.001

Determination of d.

$$d = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{S_1^2}{N_1} + \frac{S_2^2}{N_2}}}$$

The pulli of stages 1 and 2 are not significantly different from each other, but are significantly different to those of stage 3.

Table 5.2 The Size Of Pulli Recently Hatched.

Only pulli of stages 1 and 2 are considered as recently hatched (within approximately 2 hours - see text), and these are described below;

N = 178	mean	95% confidence limits
Bill length (mm.)	10.94	± 0.067
Tarsus length (mm.)	26.83	± 0.154
Weight (g.)	16.45	± 0.184

Table 5.3 Correlation Analysis Of The Size Parameters Of Pulli Recently Hatched.

Simple Correlation Matrix.

		Bill length.	Tarsus length.
Tarsus length,	r	0.353	
	P	<0.001	
Weight,	r	0.408	0.467
	P	<0.001	<0.001

Partial Correlation Matrix.

		Bill length.	Tarsus length.
Tarsus length,	r	0.202	
	P	<0.01	
Weight,	r	0.294	0.378
	P	<0.001	<0.001

The bill length, tarsus length and weight are all highly significantly, positively correlated with each other, even when considered independently by partial correlation.

Further, the correlations of the three parameters of pullus size are given in Table 5.3 , together with the partial correlations. The bill length, tarsus length and weight are all highly significantly correlated with each other, even when considered independently in the partial correlation analysis.

The size of a pullus at hatching is potentially most directly influenced by the size of the egg from which it hatched, and the correlation matrix of egg size with pullus size is given in Table 5.4 , together with a regression analysis. The three parameters of pullus size are significantly, positively correlated with the three parameters of egg size (this was greatest with egg volume). Following from this, and the significant, positive correlation of female size (wing, bill and tarsus) with egg volume shown in Section 4.3.4 , a further analysis of female size and mean pullus size is computed in Table 5.5 . Overall, the wing length of the female best explained the variance in mean pullus size ; bill length (27.4%), weight (17.7%) and tarsus length (16.2%).

As with the eggs, the variation of pullus size at hatching, within and between clutches (broods) is investigated, but because only pulli of stages 1 and 2 , from broods of four are considered, the sample is greatly reduced. The analysis given in Table 5.6 indicates that weight is the only size parameter (of the three) with significantly greater variation between broods,than within.

Table 5.4 The Relationship Between Egg Size And Pullus Size.

Seventy eight pulli were measured while still not dry from hatching and were known to have come out of a particular egg, these are analysed below;

Correlation Analysis.

Egg size parameter.		Length	Width	Volume
Pullus size parameter.				
Bill length,	r	0.416	0.442	0.544
	P	< 0.001	< 0.001	< 0.001
Tarsus length,	r	0.409	0.483	0.569
	P	< 0.001	< 0.001	< 0.001
Weight,	r	0.506	0.765	0.817
	P	< 0.001	< 0.001	< 0.001

All pullus size parameters are most highly correlated with egg volume, and the following regression analyses are computed with egg volume (EV in $cm.^3$) as the independent variable.

pullus bill length(mm.) = 0.200(EV) + 6.77
F = 32.00 P < 0.0001

pullus tarsus length(mm.) = 0.530(EV) + 16.09
F = 36.31 P < 0.0001

pullus weight (g.) = 0.864(EV) - 1.17
F = 152.40 P < 0.0001

Table 5.5 The Relationship Between Pullus And Maternal Size.

A significant correlation between egg and maternal size, and similarly between egg and pullus size, indicates that a similar relationship might exist between pullus and maternal size. This is investigated with the 25 females (sexed by the 'M.E.V. method'), that produced one or more pulli that were measured shortly after hatching (before they were fully dry). The mean size of each females' pulli is compared with the last measurement of the female.

Correlation Analysis.

Maternal Size Parameter		Chick Size Parameter. Bill	Weight	Tarsus
Weight,	r	0.009	0.214	0.039
	P	n.s.	n.s.	n.s.
Wing length,	r	0.523	0.421	0.403
	P	< 0.01	< 0.05	< 0.05
Bill length,	r	0.287	0.339	0.198
	P	n.s.	n.s.	n.s.
Tarsus len.	r	0.471	0.374	0.411
	P	< 0.02	n.s.	< 0.05
Tarsus wid.	r	0.099	0.112	-0.020
	P	n.s.	n.s.	n.s.

Clearly, the best indication of a females' mean pullus size at hatching is her wing length (FWL in mm.), and the associated regression analyses are;

mean pullus bill length (mm.) = 0.046(FWL) + 3.07
$F = 8.67$ $P = 0.007$

mean pullus weight (g.) = 0.112(FWL) - 2.51
$F = 4.95$ $P = 0.036$

mean pullus tarsus length (mm.) = 0.087(FWL) + 12.08
$F = 4.47$ $P = 0.046$

Table 5.6 The Analysis Of Variance Of The Size Of Pulli Recently Hatched In Broods Of Four.

Only nine broods of four pulli were found in which all pulli were classed as recently hatched (stages 1 and 2 only), but these enable one way analyses of variance of the three size parameters.

Bill length.

source	df	SS	MS	F	P
Among broods	8	1.39	0.174	1.19	>0.1
Within broods	27	3.96	0.147		
Total	35	5.35			

Tarsus length.

source	df	SS	MS	F	P
Among broods	8	5.86	0.733	0.86	>0.1
Within broods	27	23.09	0.855		
Total	35	28.96			

Weight.

source	df	SS	MS	F	P
Among broods	8	36.59	4.57	7.01	<0.001
Within broods	27	17.62	0.65		
Total	35	54.21			

Weight is, therefore, the only size parameter (of the three) with significantly greater variation between broods, than within.

5.3.2 Development During The Pre-fledging Period.

The description of the change in size of pulli with age is important as a means of ageing pulli, and in providing a comparison with other populations and species.

Weight loss after hatching.

It has already been demonstrated that pulli only recently hatched are significantly heavier than those fully dry from hatching. This weight loss is investigated further over the period from hatching until the hatching weight is more than regained (that is, 110 hrs. old).

The three catagories of pulli in the nest (see Section 5.3.1) are initially treated separately as follows, to make the most of the limited available data;

stage 1 - the hatch weight is assumed to be the measure at 0 hrs. and all subsequent weights are used.

stage 2 - only the subsequent weights taken more than 12hrs. old are used, and the hatch weight is assumed to be 0.1g. greater than the first weight, 2hrs. before.

stage 3 - only the subsequent weights taken more than 24hrs. old are used, and the hatch weight is assumed to be 0.3g. greater than the first weight, 10hrs. before.

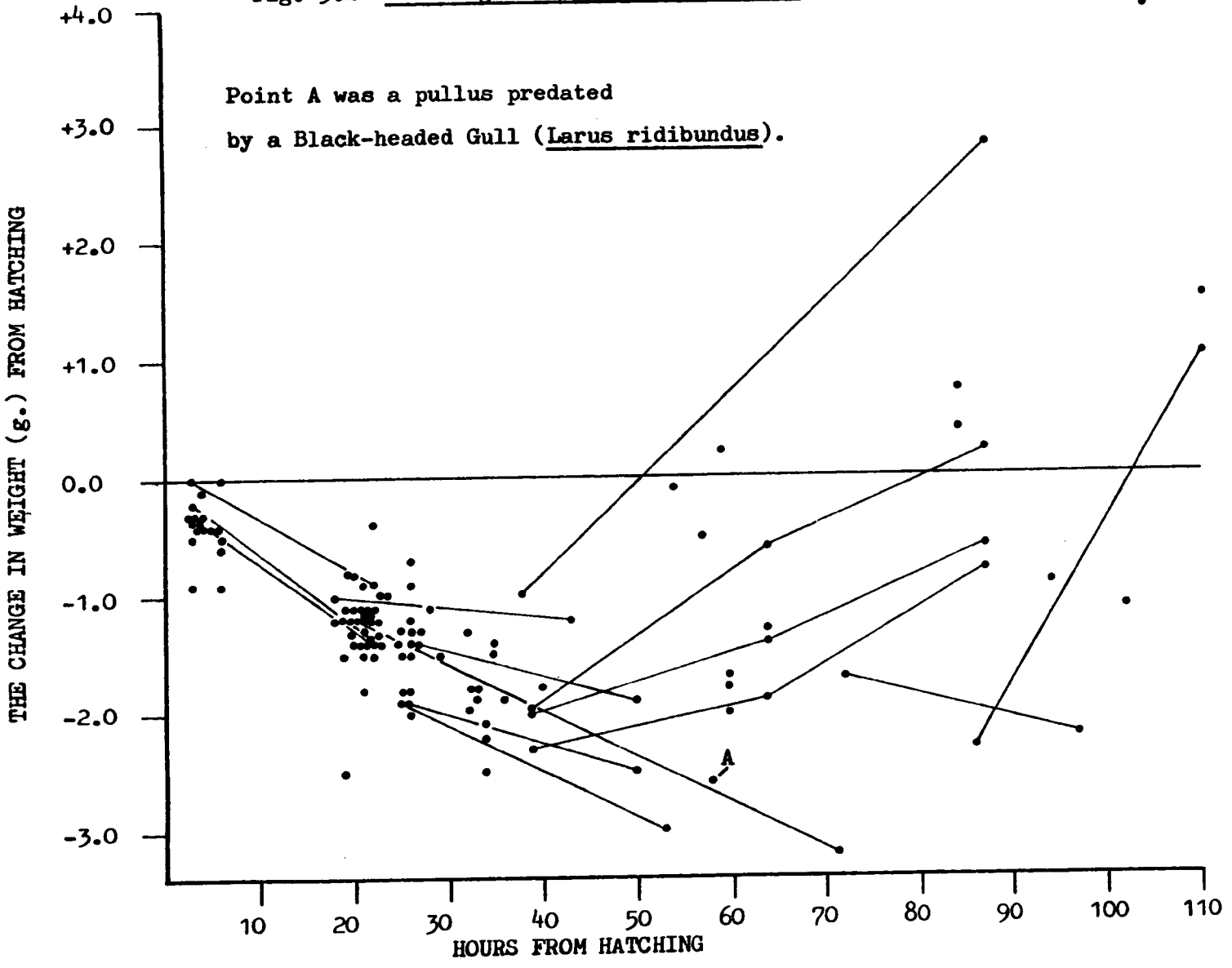
These are then combined in Fig. 5.2 , which shows three main phases of the change of weight;

phase 1 - most individuals lost a weight of approximately 2.0g.in the first 36hrs. after hatching.

phase 2 - some individuals continued this decline, while others showed some recovery. This is indicated by the increase in the variation of weight loss after approximately 36hrs.

phase 3 - the weight of recovering individuals increases

Fig. 5.2 The Weight Loss After Hatching.



above the hatching weight.

The earliest recovery of the hatching weight was observed at 58hrs. after hatching. The oldest individual observed below hatching weight was 101hrs. old.

The individual reweighed just after being seized by a Black-headed Gull (Larus ridibundus) is seen in Fig. 5.2 (point A) to have lost more weight than the average pullus of its age.

Other aspects of growth.

From pulli of known age (that is, ringed in the nest), it was possible to draw up a growth curve for the bill which, for the six days after hatching, a large sample showed a rapid linear increase. This enabled some birds of unknown age, to be aged (see later, for a fuller consideration of this topic).

In the complete growth curves the first measures of these 'aged' pulli is omitted, because thay are determined directly from the initial growth curves. The subsequent measures are added to those from birds of known age, to produce the three growth curves of bill, weight and tarsus, which are given in Figs. 5.3 , 5.4 and 5.5 respectively. Fig. 5.6 summarises these by showing only the daily means and indicating the lines giving the best fit. The mean adult size is also shown for comparison.

During bill development, an almost linear rate of increase is observed, that shows a slight slowing towards the age of fledging. However, a linear regression through the daily means gives a good fit;

Bill length (mm.) = 0.62 x Age (days) + 11.28

During weight development, the initial weight loss investigated before is again seen, and then the more variable data suggests a rapid

Fig. 5.3 Development Of The Bill During The Pre-fledging Period.

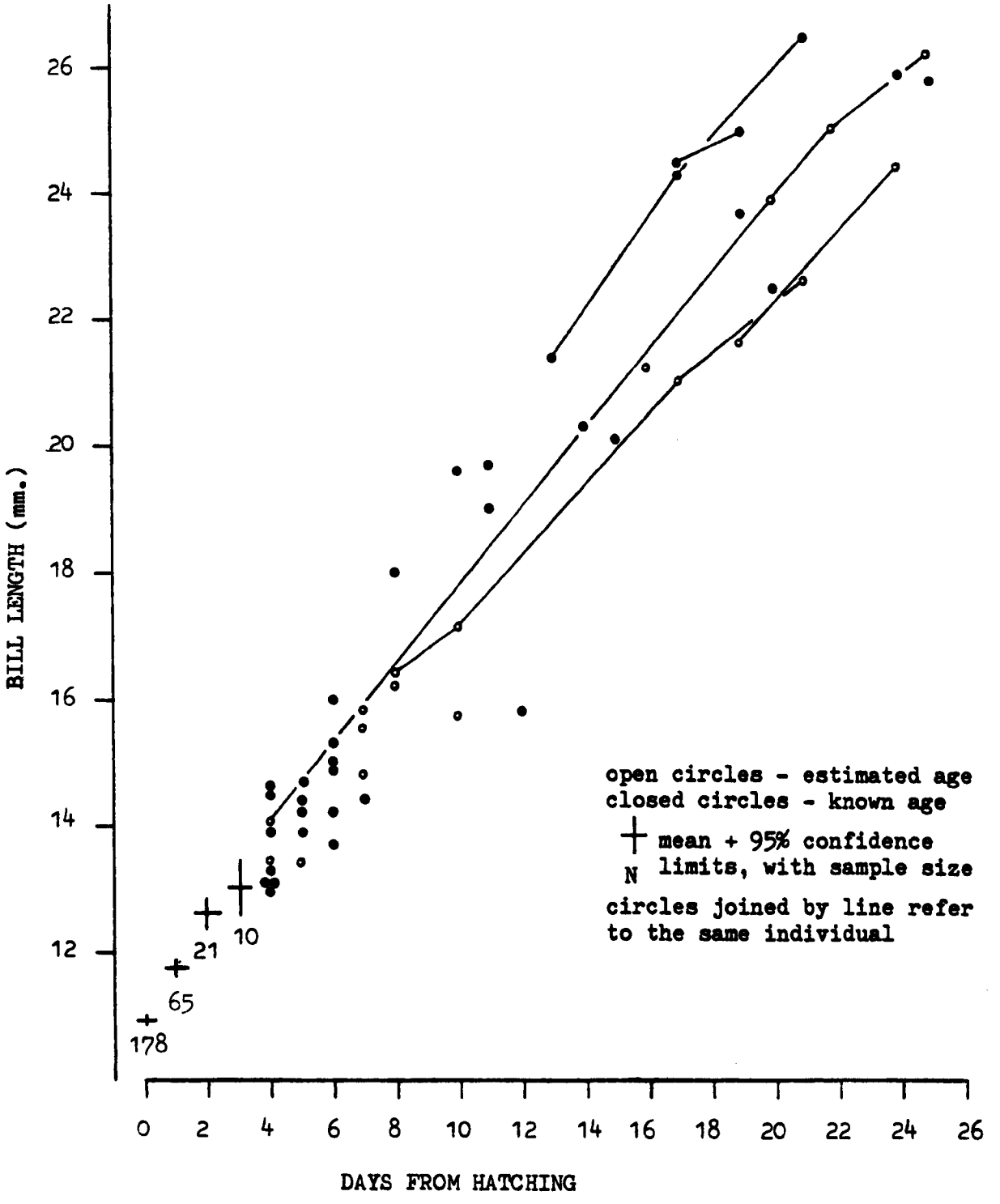


Fig. 5.4 Development Of Body Weight During The Pre-fledging Period.

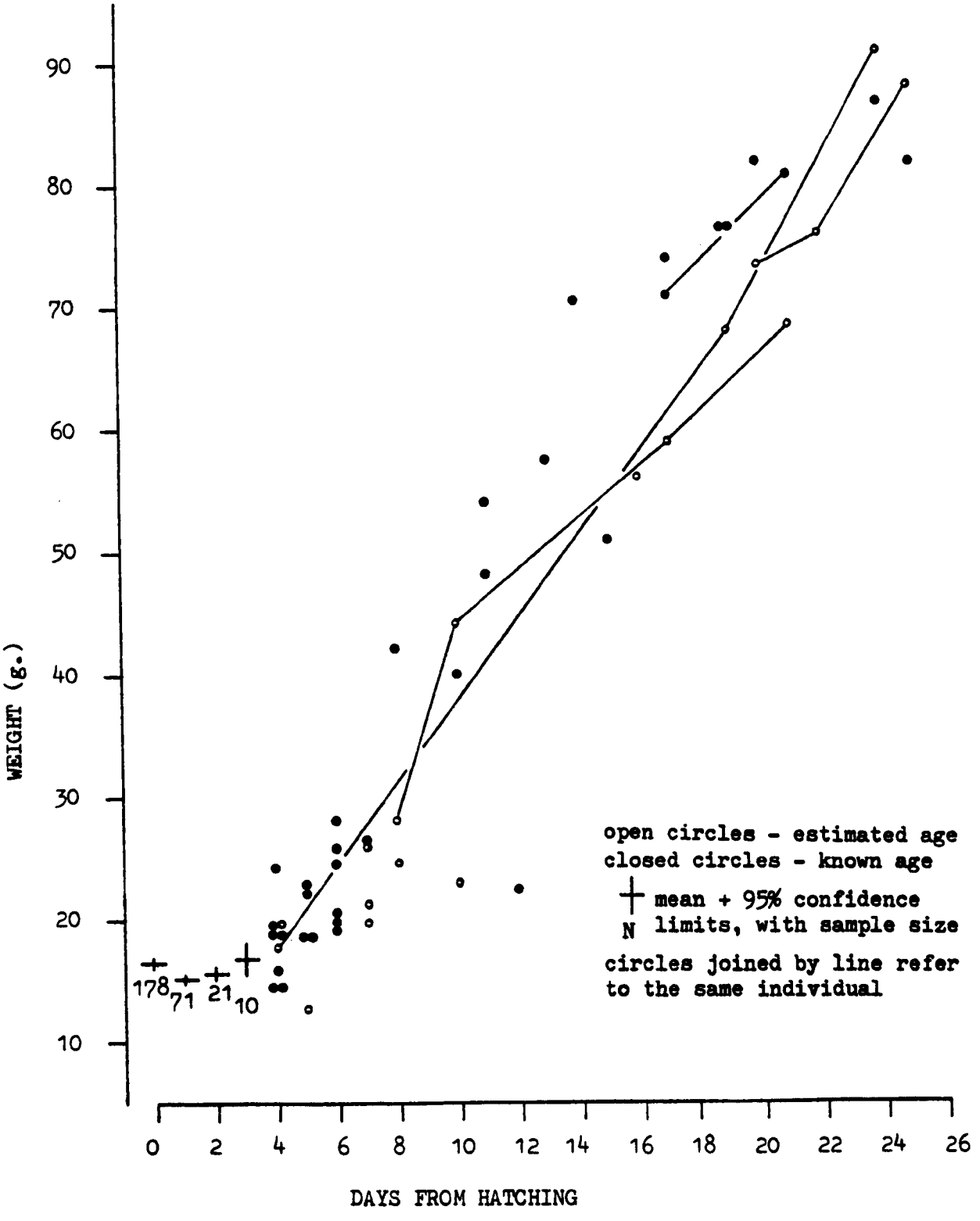


Fig. 5.5 Development Of The Tarsus During The Pre-fledging Period.

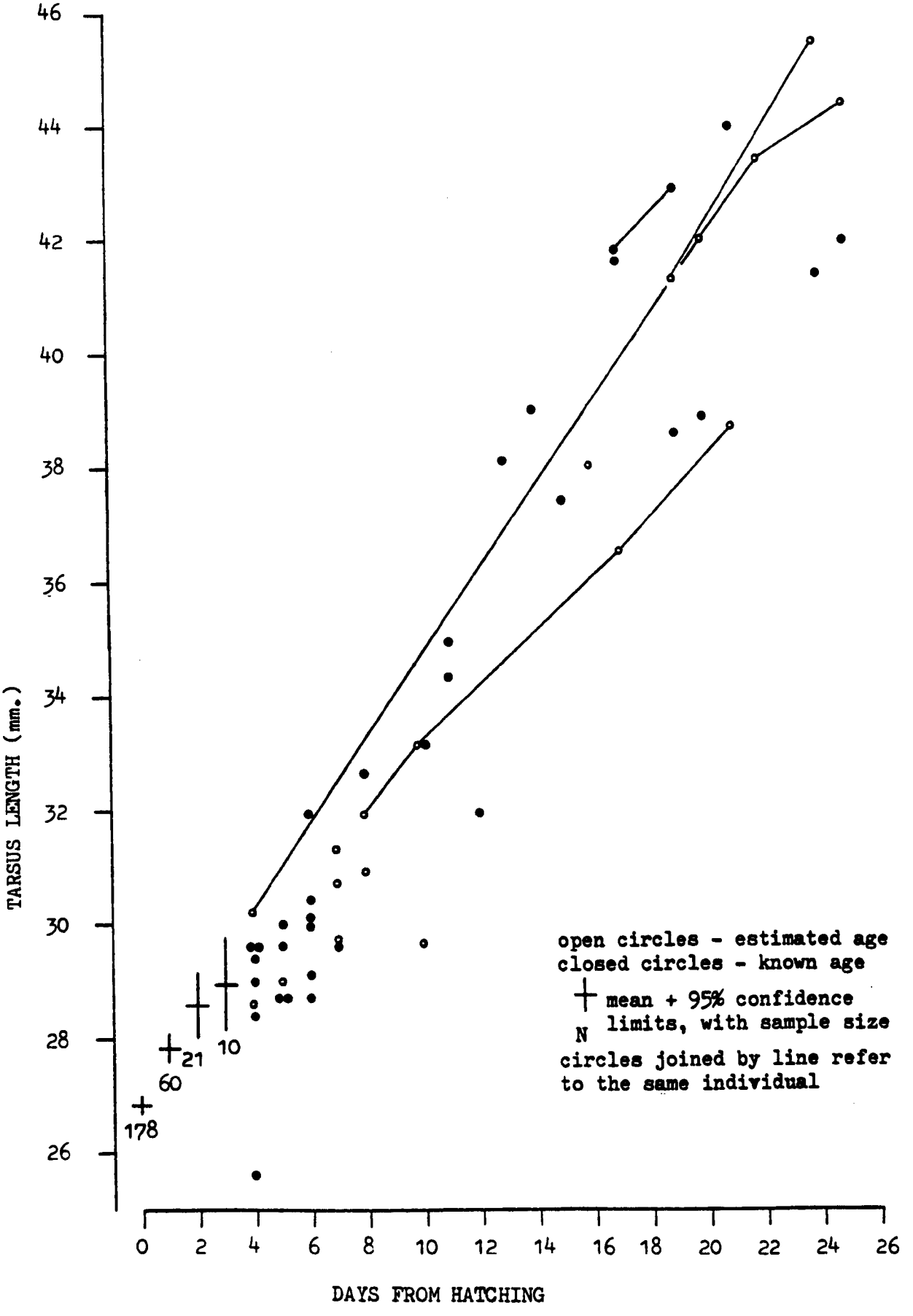
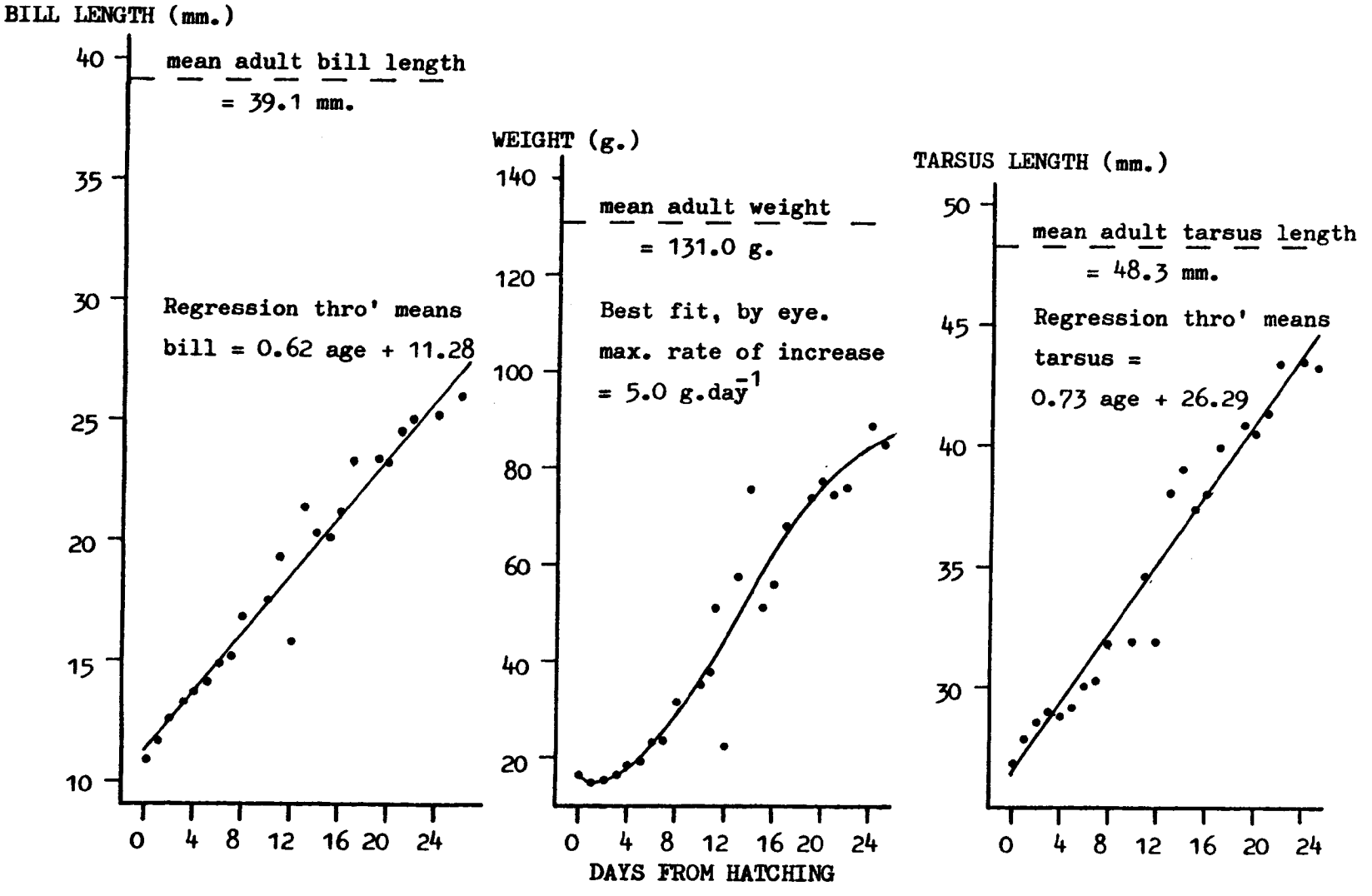


Fig. 5.6 A Summary Of The Growth Curves For Bill Length, Weight And Tarsus Length.



increase (of approximately $5g.day^{-1}$), that slows towards the age of fledging.

During tarsus development, a similar pattern to the bill development is seen. However, an apparent decline in the rate of increase during the age of 4 to 6 days, represents a great difference to the bill. Overall the increase in tarsus length is $0.7mm.day^{-1}$.

Another presentation of these growth curves expresses the pullus measurements as a percentage of the mean adult measurements, and this enables a direct comparison between the size parameters, which appear on one graph in Fig. 5.7 . In comparison with the adult size the pulli at hatching are very light (13% of adult) with an intermediate relative bill length (28%) and very long tarsi (55%). By twenty-five days old the weight (65%) approaches the relative size of the bill (66%), but the tarsus development is most advanced, at 90% of the adult length.

The oldest individuals measured were 25 days after hatching, and fledging is considered to occur at, or shortly after, 27 days. Therefore, the pulli close to fledging are the following proportions of the mean adult size;

$$\frac{\text{fledging size}}{\text{mean adult size}} = 0.67 \text{ bill length}$$

$$= 0.69 \text{ weight}$$

$$= 0.92 \text{ tarsus length}$$

or, expressed as the fledgling change in size from hatching, as a proportion of the adult change in size from hatching;

$$\frac{\text{fledgling size - hatch size}}{\text{adult size - hatch size}} = 0.54 \text{ bill length}$$

$$= 0.64 \text{ weight}$$

$$= 0.78 \text{ tarsus length}$$

Fig. 5.7 The Growth Of Pulli Relative To The Adult Size.

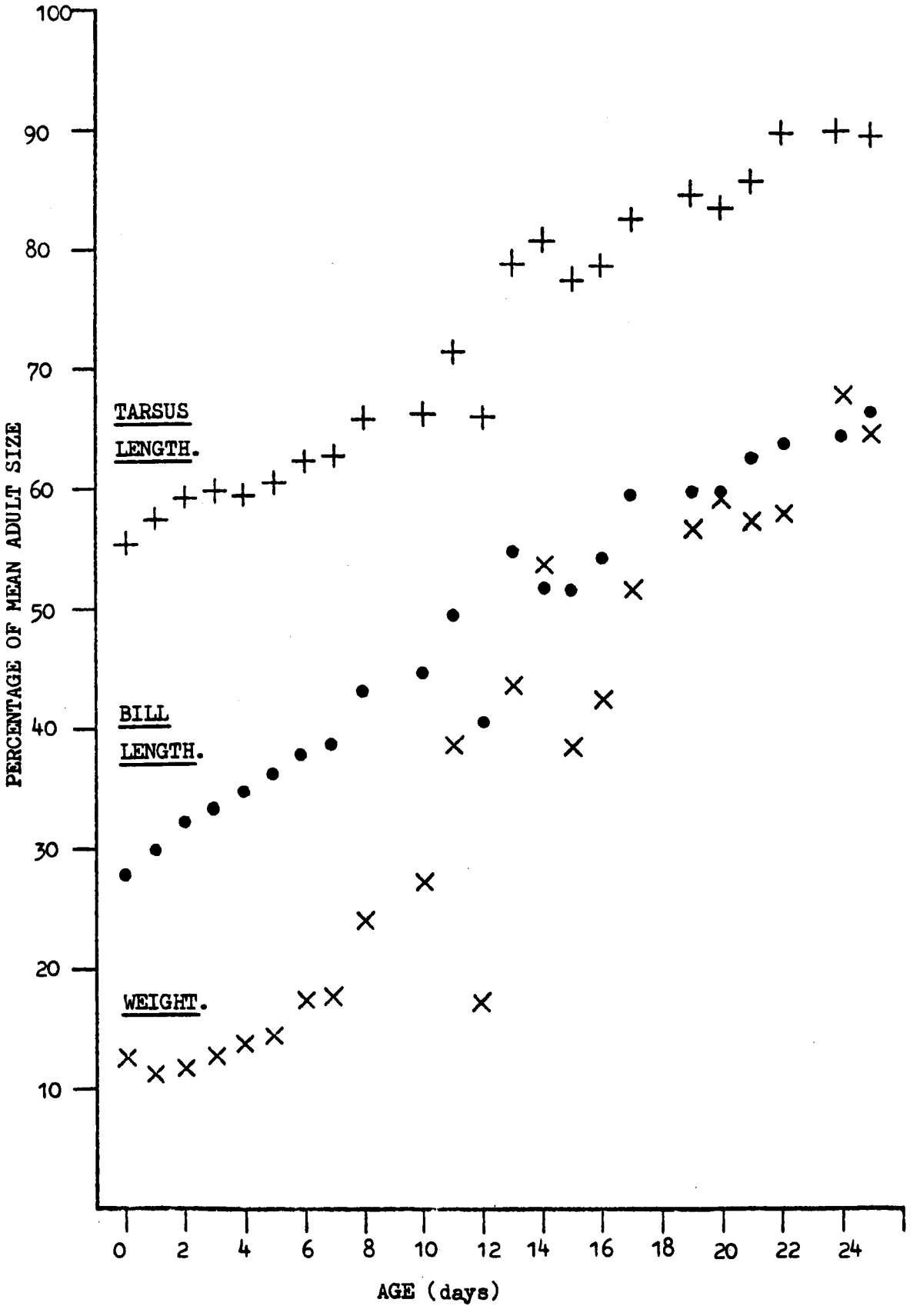


Table 5.7 The Size Parameters Of Pulli As Criteria For Estimating Their Age.

Size parameter	Advantages.	Disadvantages.
Bill length.	a) an almost linear increase. b) a rapid increase. c) variation at hatching is not significantly greater between broods. d) the least variable parameter.	a) requires care in measuurement although the technique is quickly mastered.
Weight.	a) easily measured.	a) very variable because it partly represents 'body condition', which can both increase & decrease. b) variation at hatching is significantly greater between broods. c) the 'increase' is not linear.
Tarsus length.	a) variation at hatching is not significantly greater between broods.	a) more variable than bill. b) increase is not so linear as bill length. c) requires care in measuure--ment, although the technique is quickly mastered.

Therefore, the bill length is considered the most appropiate of the size parameters for determining the age of Redshank pulli.

Therefore, the growth of the Redshank has only been partly investigated above, because close to fledging the pulli are still considerably smaller than the adults. Extrapolation of the linear increases of bill and tarsus lengths (see Fig. 5.6) give an adult size by 45 days (bill) and 30 days (tarsus), but this,of course, assumes the same rate of increase after fledging.

The ageing of pulli.

The three growth curves produced could each estimate the age of a pullus, but consideration of just the most suitable one would be of more value. The merits of each is considered in Table 5.7. After considering Table 5.7 , it is clear that the bill length is the most appropiate parameter for determining the age of Redshank pulli, and that the following equation is a good estimate;

$$\text{Age(days)} = \frac{\text{Bill length(mm.)} - 11.28}{0.62}$$

Great care must be taken if this method is used for other populations, since it is not known if the rate (0.62) or the intercept (11.28) of the growth curve are different in other populations or habitats. The intercept probably differs between populations because of its dependence on the mean egg size (see Section 5.3.1 , Table 5.4), which varies greatly between populations (Vaisanen, 1977).

The postnatal moult.

Immediately after hatching the pulli are covered with downy plumage that is wet, but after two hours this dries out and becomes fluffy. This downy plumage serves two functions, firstly as an insulating layer, and secondly as cryptic colouring.

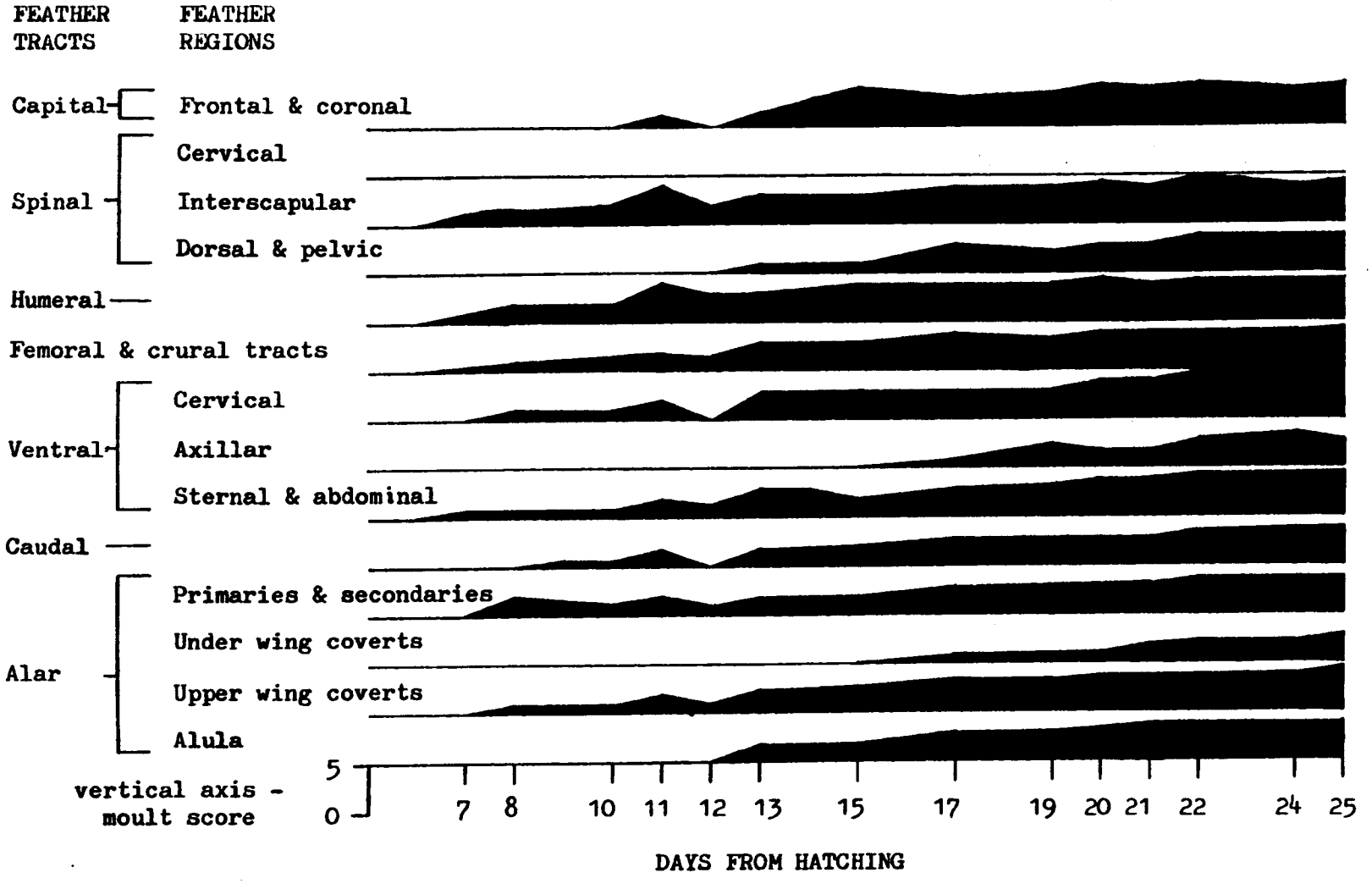
During development of the pulli this plumage is replaced by the juvenile plumage, that facilitates flight and gives greater protection from adverse environmental conditions. The loss of the

downy plumage, and the development of the juvenile plumage was termed the postnatal moult by Holmes (1966b).

This moult is seen, in Fig. 5.8 , as a gradual process, and the timing of the visible feather development differs between the feather regions (and even within a feather region, although this is not investigated).

By eight days old juvenile feathers of two types are appearing, firstly, those aiding flight, and secondly, those providing insulation. In contrast, those regions covered by the closed wing (axillaries and under wing coverts) are late in appearing, at seventeen days. At the time of fledging there is no visible. development of the juvenile feathers in the spinal tract - cervical region, and this is still downy, while most other feathers are nearly their full length, and therefore, almost fully functional.

Fig. 5.8 The Postnatal Moult.



5.3.3 Movements Of Broods During The Pre-fledging Period.

The determination of the distances moved by broods from the nest is important for the consideration of pre-fledging mortality (see Section 5.4), and in the general breeding biology of the species. It may also be important in census methods that rely on the number of broods to estimate the population size; if the broods are highly mobile they could be counted more than once.

The capture of pulli was largely concentrated within the Restricted Area, and therefore the analysis of movements is biased to those broods staying within the area, that is, extreme movements are underestimated.

The distance moved by individual broods from the nest, as revealed by recaptures, is shown in Fig.5.9. This clearly indicates that there is an initial large movement away from the nest, and then less extreme movements up to fledging. However, the variation between broods is great.

This trend is further seen in Fig. 5.10 , which maps the position of broods captured more than twice. Brood K and G clearly show the trend outlined above, but A,B,D,E and H are still within 100m. of the nest more than four days after hatching.

The general trend is for the brood to move quickly to an area after hatching, which is presumably rich in food and provides shelter from predators, where they can become locally experienced in feeding and hiding. For most broods this 'favoured' area was a medium sized channel, approximately 1 to 2m. wide.

Fig. 5.9 Movements Of Broods Away From The Nest.

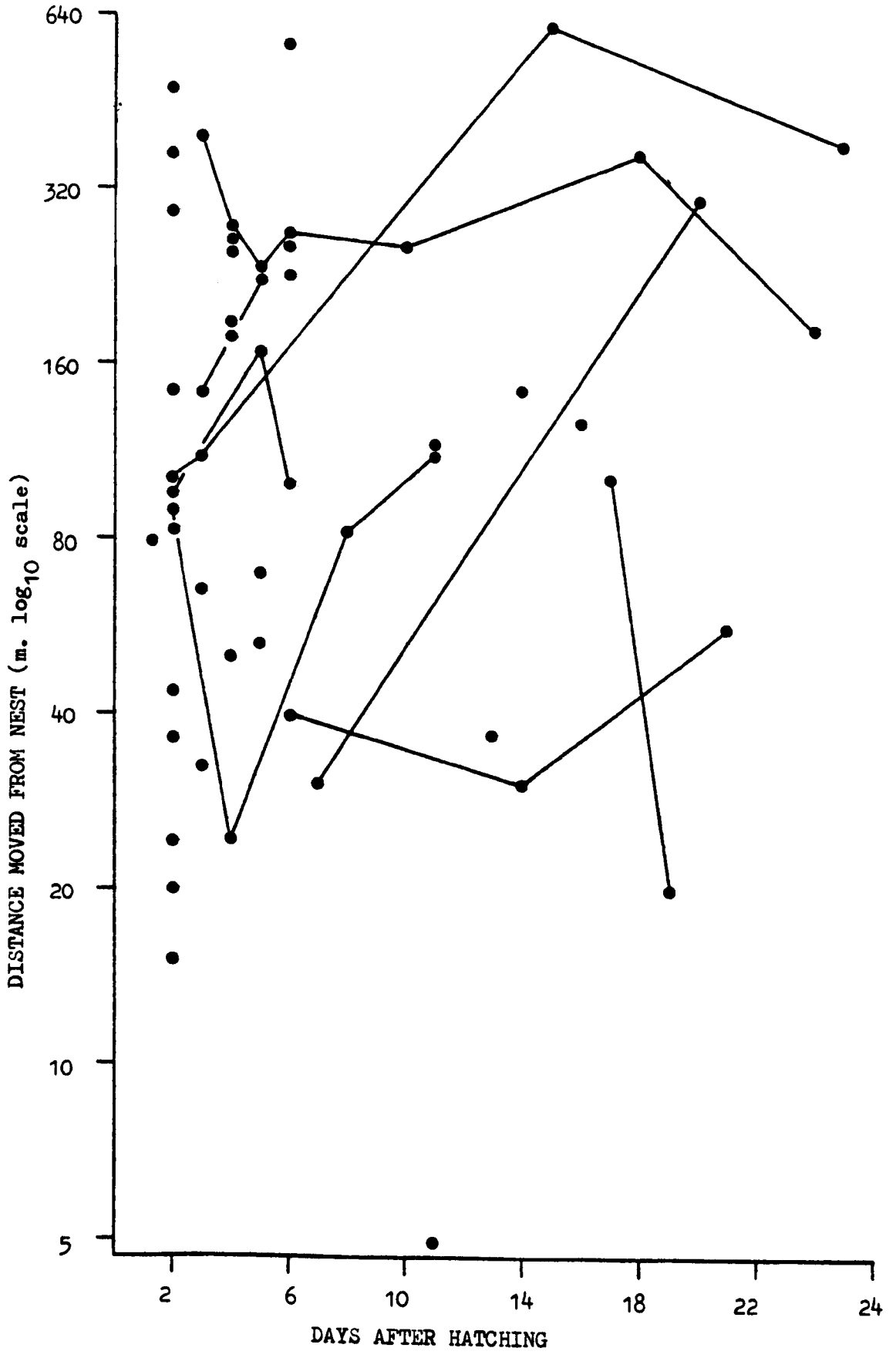
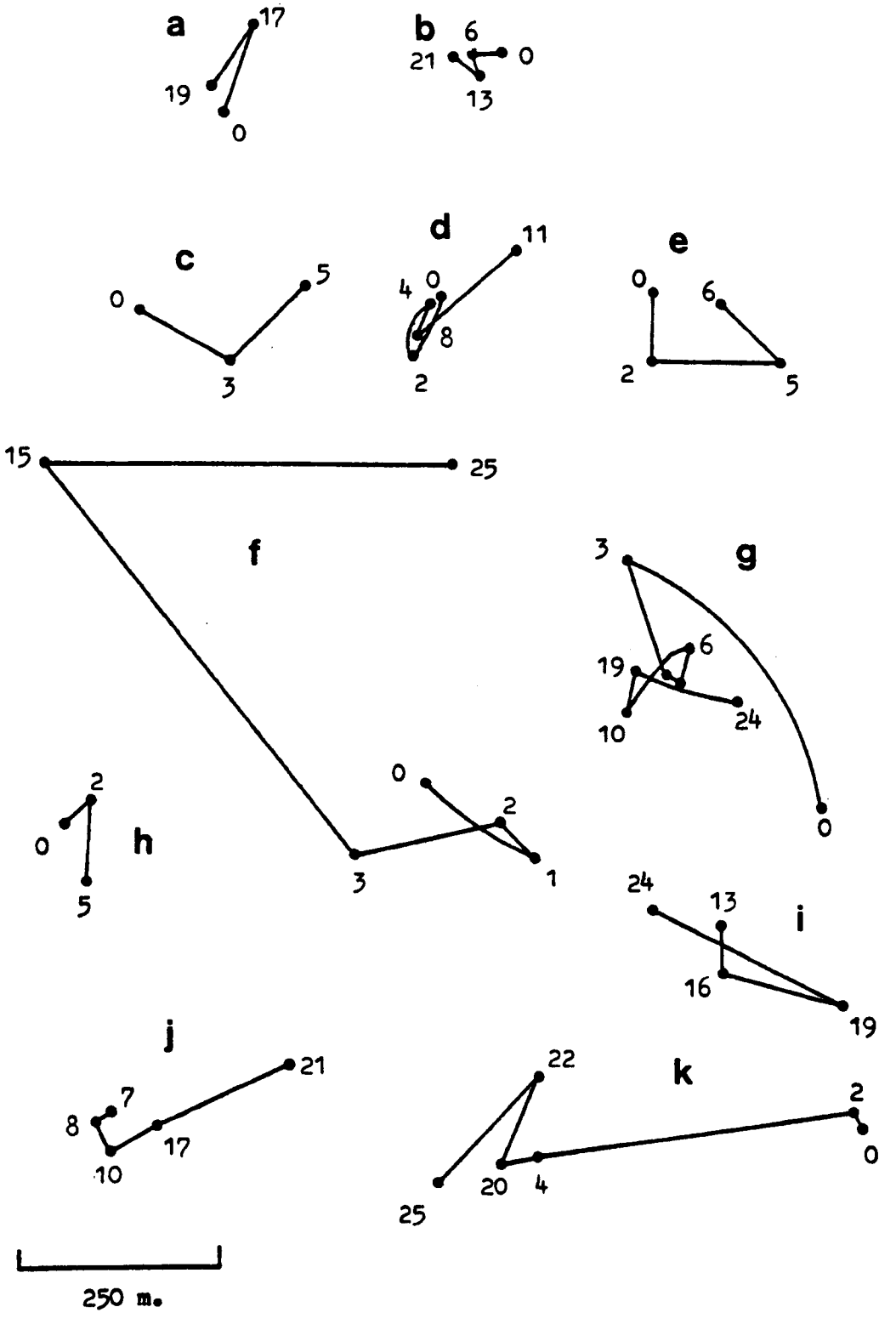


Fig. 5.10 The Movements Of Broods Caught On More Than Two Occasions.

Sites of capture are only related within a brood, and not between broods.



5.3.4 The Breeding Of Pulli Hatched Within The Study Area.

Grosskopf (1963) recorded only 3.2% of pulli hatched in his study area, returning to breed in subsequent years, and he considered (Grosskopf, 1964) that the age of first breeding was most commonly two years, despite several cases of breeding at one year old. Ashcroft (1978) reported no pulli returning to this study area to breed.

Seven pulli out of 555 ringed in the present study area before 1981, returned to breed, and their ages at first breeding are shown in Table 5.8 . This clearly demonstrates that the Redshank commonly breeds at one year old.

The very low rate of known return of pulli to breed (less than 2%) indicates that either mortality is very high, or that fidelity to birth site is low, such that individuals do not return exactly to the study site. In either case the breeding population is maintained by immigration.

Table 5.8 The Number Of Pulli Ringed In The Study Area, And The Number Returning To Breed.

The number of pulli ringed throughout this study was;

YEAR	1974	1975	1976	1977	1978	1979	1980	1981	Total
NUMBER RINGED	32	51	47	18	76	147	177	162	717

The individuals known to return and breed were;

RING NUMBER.	DATE HATCHED.	DATE OF CLUTCH COMPLETION OF FIRST NEST.	AGE (years).
DR80827	29-6-1979	24-4-1980	0.82
DR52792	14-6-1979	24-4-1980	0.86
DR36390	17-6-1979	17-5-1980	0.92
DR97304	21-5-1980	14-5-1981	0.98
DR52575	28-5-1978	8-6-1979	1.03
DR52535	17-7-1979	3-6-1981	1.88
DR13864	3-6-1974	12-6-1981	7.02

5.4 Discussion.

The growth and development of wader pulli under natural conditions has previously recieved little attention. These factors may be important in understanding the overall population dynamics of the species, since they may indicate periods of great stress on the pulli.

The size at hatching (as estimated by bill and tarsus lengths, and weight) was correlated with maternal size, and although this was the first time this relationship has been directly shown for waders, it was an expected result. This followed from the separate correlations of egg and pullus size (for example, Dunlin Calidris alpina , by Soikkeli, 1967, p.167 , and Ringed Plover Charadrius hiaticula , by Green, 1978b, p.111), and of egg and maternal size (for example, several wader species by Vaisanen et al 1972) which had previously been demonstrated. These other relationships were also demonstrated for the Redshank in this study.

From the correlation between egg volume and pullus size at hatching, and the great variation in mean egg volume in different populations described by Vaisanen (1977), there must be a similar great variation of mean pullus size at hatching. The results of this study, therefore, can only be applied to other populations with great care.

The weight at hatching has been shown to influence the growth rate and age of fledging in some charadriiform birds. For example, in the Sooty Tern (Sterna fuscata) heavy pulli at hatching grew faster and could fly at an earlier age than the light ones (Feare, 1976), and in the Herring Gull (Larus argentatus) growth rate was correlated with hatching weight (Davis, 1975). This initial

size may also be an important factor in Redshank growth and survival, because, again in the Herring Gull, Parsons (1970) reported that, "an appreciable part of the size (weight) difference in newly hatched gulls, is caused by yolk retained within the chick at hatching," and the pulli with lower yolk reserves suffered a higher mortality in the first few days.

After leaving the nest the pullus's priority is to learn to find and handle food, before the body reserves are fully depleated. This is the period when many individuals showed continued weight loss, and were most susceptible to body cooling (because of their small size) and predation. The pullus that was observed to be taken by a Black-headed Gull (Larus ridibundus) is a tentative indication that the lighter (in weight) pulli may be preferentially predated (probably bacause they can remain cocealed for shorter periods than well nourished pulli).

In other waders bad weather reduced the available food and resulted in a higher pullus mortality (Holmes, 1966) and the risk of predation was greater for young Haematopus spp. when food was scarce (Harris, 1967 and Safriel, 1967). Bad weather may also kill pulli directly, especially in the few days after hatching, when they are most vulnerable to chilling and disappeared fastest (Soikkeli 1967, Parmalee, 1970 and Heppleston, 1972).

The additional stress imposed by the development of the juvenile plumage began at about the age of eight days (and continued beyond fledging), but it did not appear to slow the growth of the pulli. In fact this is when the weight gain was greatest, indicating that the pulli by this age were able to obtain the extra food for the formation of this new plumage. Of course, those pulli that were

unable to feed sufficiently either died or showed a slower development (see the 12 day old pullus on the growth curves - Fig. 5.3, 5.4, and 5.5 - that had the bill length of a 7 day old, the weight of a 5 day old, the tarsus length of an 8 day old and a postnatal moult that was also backward). Such a slower development would increase the pre-fledging period and therefore, reduce the chance of fledging.

Ashcroft (1978) investigated pullus development, but used a very small sample that included very few pulli of known age. He determined a 6-7% weight loss up to the second day of life, which was less than that found in the present study (2.0g. lost by an average pullus of 16.5g. = 12.2% loss, 36hrs. after hatching), possibly because his sample consisted of all pulli in the nest, rather than those that had recently hatched. He also probably overestimated the pre-fledging period at 33 days, because his sample consisted mainly of pulli of estimated age (and his day of hatching was termed day 1, and not day 0).

In common with other precocial pulli (Ricklefs, 1979) the Redshank hatches at a functionally advanced state of maturity, and is large (13% of adult weight); in particular the legs are relatively massive (56% of adult length) because they are important in feeding and in avoiding predators. The bill is as long as it could be within the constraints of the egg size (28% of adult length), but cannot be used efficiently for the probing feeding typical of the adult. Shortly after hatching, feeding consists mainly of pecking at small, visible, moving prey, but as the length of the bill increases, feeding in water begins and finally probing in mud becomes the major mode of feeding (personal observations). The timing of these events in relation to the bill length is, however, unknown.

The detailed description of growth and development of the

Redshank can only be compared with one other wader species studied in similar detail, the Dunlin. Soikkeli (1967) studied the growth, and Holmes (1966b) the postnatal moult of this species with a pre-fledging period of approximately 21 days. It shows good general agreement with the Redshank, but the decline in weight of the Dunlin after hatching lasted only approximately 24hrs. This may result from most of the pulli being fully dry at their first weighing, but it could also reflect their smaller size and more rapid development, or habitat differences (see below). The bill length of Dunlin was more variable in older pulli, when compared with the Redshank but this was due to the sexual dimorphism of the adult Dunlin, not seen in the Redshank. The postnatal moult of the Dunlin began in the same areas (of humeral tract and interscapular region) as the Redshank but a little earlier, within a week, rather than eight days. The important development of the flight feathers, however, is much later in the Dunlin; breaking sheath occurs at 15 days old, compared to before 13 days in the Redshank, but in both, the first flights were undertaken before the completion of the feather development.

The weight change of the pulli of Lapwing Vanellus vanellus was studied by Jackson and Jackson (1975), and although a weight loss after hatching was not determined, there was a slow increase at this time.

Five species of wader (including Dunlin) were studied in Arctic habitats in sufficient detail to provide approximate growth rate data (Green, 1978, p. 123). The range of mean relative growth rate, r [**1] was 0.0827 to 0.1462 $g.g.^{-1}day^{-1}$, much higher than that seen in this study for the Redshank of 0.065 $g.g.^{-1}day^{-1}$, which would seem to reflect the differences in the habitats. In the Arctic

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[**1] $$r = \frac{\log_e (\text{fledging weight} \div \text{hatching weight})}{\text{fledging period}}$$

nesting birds the hatching period coincides with a great abundance of food (for example, Holmes, 1966 , p.37) which does not occur, to the same extent, at this study site.

In captivity, individuals of a brood of Redshank showed a different pattern of growth from that seen here (Goss-Custard et al 1971). From 7 to 21 days old a similar rate of increase in weight was seen, but at 21 days the captive birds weighed 97g. , and could fly, whereas the wild ones were only 65g. and could not. The difference was apparently due to the long period below the hatching weight in the wild birds that was not experienced by the captive ones. The mean relative growth rate of these captive Redshank ($0.0917 g.g.^{-1} day^{-1}$) was within the range of the other waders in the Arctic, and probably results from the comparable abundance of food.

It was impossible to quantify pullus mortality because of the extreme elusiveness and mobilty of the pulli, but from the apparent disappearance of most pulli in the first few days after hatching it suggested that most of them did not make up their hatching weight again. These few days therefore, probably represented the 'critical period' of survival, and the method outlined below, may provide more information on mortality.

If this study had produced an accurate estimate of pre-fledging mortality it is not known how widely this would be relevant to understanding the dynamics of all Redshank populations. A more general estimate is required that could differentiate between habitats, and this can be achieved if all Redshank pulli ringed are aged by the method given in this study.

Pulli ringed at an early age would have a lower chance of post-fledging recovery than those ringed later. The difference in recovery rates would be proportional to the mortality occuring

between the two ages of ringing.

From such a method it would be possible to consider the timing of the overall pre-fledging mortality, and also to compare ha habitats. In addition, it may be possible to investigate the post-fledging mortality in a similar manner, and to estimate these mortalities by comparison with recoveries of birds ringed as '1st year'.

Direct observation at a more suitable site could provide a site specific mortality estimate as well as an indication of the importance of weather and predators on the mortality. Such a suitable site should have the following characteristics;

a) a small area that can be totally covered.

b) a topography and vegetation that does not hinder direct observation.

c) boundaries preventing the 'escape' of broods, for example, an island.

d) a moderate sized population such that all broods can be followed.

Such a suitable site would provide great scope for further study of this important stage of the life cycle of the Redshank.

Estimation of the mortality from fledging until first breeding in the present study was impossible because of the very low rate of return (less than 2%). Such a low rate of return of pulli to a small study area is common to most studies of waders (see Vaisanen, 1977, p.21 and Soikkeli, 1970b, p.6), and probably results directly from the small study areas. In the Dunlin more than half of the reports of 'pulli' breeding were more than 2.0km. from their birth site (Soikkeli, 1970), and if a similar pattern

exists for the Redshank, very few of the surviving pulli would nest within the study area and ,therefore, be available for capture. Despite this, I consider the Redshank to be faithful to it's birth site, but the fidelity is much weaker than the strong nest site fidelity of the adults (see Section 3.3.5).

It is the combination of the strong nest site fidelity and the weaker birth site fidelity of the Redshank that facilitates the genetical differentiation of populations that is reflected in the geographical variation of the species (see Hale, 1971).

CHAPTER SIX - THE DYNAMICS OF THE POPULATION.

The dynamics of this population was not completely studied, but tentative estimates of the missing components (pre- and post-fledging mortality) can be made.

Emigration of adults, especially males, was slight, and so the overall survival rate of 0.77 was considered to be an accurate estimate. To remain stable, therefore, the population required an annual recruitment of 0.23 to balance the loss of breeding adults. The population had, however, declined by approximately 0.35 in five years, that is, 0.08 per annum, so recruitment was approximately 0.15 (= 0.23 - 0.08). This recruitment was considered to come mainly from outside of the study area, that is, the population in the surrounding grazed saltmarsh (see Section 5.3.4).

The inability of this larger population to maintain a stable level in the study population indicated that it was in difficulty in producing sufficient pulli. The production of pulli in this surrounding population is assumed to be the same as in the study population. Adults breeding in their first year began breeding mainly late in the season (see Section 3.3.4), and were not, therefore, usually able to replace failed nests. In contrast, the experienced breeding adults began early and were able to replace failed nests. The different estimates of pullus production of Section 2.3.6 were, therefore, applicable to these two distinct groups.

From recovery data of ringed birds the post-fledging mortality of juveniles of European waders ranged from 1.2 to 2.5 (mean 1.6) times as high as the annual mortality of adults (Boyd, 1962). This mean figure will be used in preference to the figure

of 0.55 estimated from ringing data (also in Boyd, 1962), because it has previously been shown that this latter method generally overestimates losses (see Section 3.4, especially Table 3.24). For the Redshank, therefore, the estimate is 0.37 (= 1.6 x 0.23) for the proportion of pulli that fledged that did not survive to breed.

The missing component of the dynamics of this population, the pre-fledging mortality, is estimated from a model that included all of the above factors, and it is described in Table 6.1. Using this model with the pullus production estimates of the grazed saltmarsh, the pre-fledging mortality was manipulated until the simulation resembled the observed parameters of the population, with respect to the recruitment and population change. A satisfactory simulation was achieved with a pre-fledging mortality of 0.67. After five years this provided a recruitment of 0.15 and a population decline of 0.25. Other workers' estimates of pre-fledging mortality were incorporated into the model, and generally, these were too low, giving high recruitment and therefore, insufficient population decline (see Table 6.2).

With the best pre-fledging mortality estimate of 0.67, it is possible to predict the benefits of preventing grazing during the nesting season. The increased production of pulli (see Table 6.1) resulted, after five years, in recruitment of 0.22 and a population decrease of just 0.02.

The simple control of cattle during the nesting season would, therefore, mean the difference between a declining population, and a stable one.

It must again be emphasized that this model is far

Table 6.1 A Model Of The Population Dynamics.

Proportion of '1st year' breeding adults = A1, initially = 0.15.

" 'experienced' " = A2, initially = 0.85.

Relative size of breeding population = BP = A1 + A2.

Pullus production of '1st year' adults = P1 per adult.
" 'experienced' " = P2 per adult. } from Table 2.12

In grazed areas, P1 = 0.47, and P2 = 0.79

In ungrazed areas, P1 = 0.86, and P2 = 1.14

Pre-fledging survival = PF

First year survival = FY = 0.63 (from Boyd, 1962)

Mean number of pulli hatched, per adult. $= HP = \left(\frac{A1}{BP} \times P1\right) + \left(\frac{A2}{BP} \times P2\right)$

Mean number of pulli surviving to breed, per adult. $= SP = HP \times PF \times FY$

In the following year;

$A2 = BP \times 0.77$

$A1 = SP$

Table 6.2 The Results Of The Population Model.

Simulating the population, with the pullus production estimates for grazed areas, gave the following results after 5 years;

Source of the pre-fledging mortality estimates.	Estimate.	Recruitment.	Population change.
Ashcroft (1978)	0.22	0.35	+0.37
Grosskopf (1964)	0.50	0.23	-0.01
Nordberg (1950)	0.59	0.19	-0.13
This study.	0.67	0.15	-0.25

The estimate of this study was made by manipulation of the pre-fledging mortality, until the behaviour of the model resembled the populaton with respect to recruitment and population change.

removed from the natural properties of the population. For example, it does not consider the replacement of lost broods (see Section 2.3.5), nor the widely fluctuating pullus production because of the occasional catastrophic nest losses due to tides. The model is just a bland averaging of observed production and losses over a relatively short period in this population's history.

Understanding the regulation and control of a population is the ultimate aim of a breeding study, but the mechanisms involved are extremely complex.

Ashcroft (1978) suggested that in this population of Redshank the density-dependent mortality of pulli, caused by the limited availability of suitable feeding areas for unfledged pulli, was the major regulating factor. My experience, in years when more pulli hatched, indicated that they could survive in many areas of the saltmarsh. For much of the 'pullus season' most of these areas were vacant, which suggested that limited suitable feeding areas was not the factor regulating this population. Further, the weak tenacity to birth site means that such a regulating factor would limit recruitment to a different part of the population.

In highly territorial species the breeding density is related to the food supply, with dispersal throughout the suitable habitat achieved by behaviour (for example, Dunlin Calidris alpina , Holmes 1970). For such populations, where recruitment is less than production, pairs are forced to breed in sub-optimal areas and other individuals are unable to breed at all. Production is, therefore, limited to the fittest individuals. The population of non-breeders acts as a buffer, to maintain the breeding population when adult mortality has been high (for example, the removal experiments of Holmes, 1966,

on Dunlin, and of Harris, 1970, on Oystercatcher Haematopus ostralegus), and to enable new areas to be rapidly colonised (for example, the case of the Temminck's Stint Calidris temminckii reported by Hilden 1978, p.26).

The Redshank, however, is unusual in that it does not show typical territoriality during the breeding season (Hale, 1956), such that nests of different pairs, at similar stages, were found very close to one another (in the present study many cases of nests less than 2m. apart). The pres ence of non-breeders in this species has not been verified because of the mobility of breeding adults and the long breeding season (such that an apparent non-breeder may be a late breeder or a failed early one). Despite this, a regulation of this population may be indicated by the recent increase in the return rate of pulli, to breed. When the population was estimated to be at its highest (in the years 1975 to 1977, see Fig. 3.12) no returning pulli were observed, but in the recent years of lower population, a few have (see Fig. 5.9, however, it is a pity that so few pulli were ringed in the early years of this study). Hilden (1978) reported a similar trend for Temminck's Stint, and interpreted the significant lower return rate as the exclusion of the returning 'pulli' from favoured areas by experienced territorial breeders.

The apparent decline in the population of Redshank was suggested, in the model above, to be due to the low nesting success because of the cattle destroying many nests. Such a decline should not have occured if there was a non-breeding population and there was no change in the habitat of the study area.

It must be remembered, however, that the saltmarsh habitat

is a transient one that subtly changes from year to year. The gradual maturing and drying process may have passed the optimal requirements of breeding Redshanks, such that the adult population has declined. Resources for egg formation and nesting were still apparently favourable, but the growth of the pulli suggested that their full requirements were not being met.

CHAPTER SEVEN - A SUMMARY

7.1 THE NESTS

The timing of the beginning and ending of the breeding seasons varied greatly, and both were highly correlated with the prevailing meteorological conditions, especially rainfall. In years of high rainfall the season began later and ended earlier, and this was considered to be due to impaired feeding and/or courtship behaviour.

Within all seasons the nests showed a highly aggregated spatial distribution, that was reflected by the distribution of the preferred nesting vegetation, Festuca rubra. The temporal distribution of clutch completion dates showed a multimodal frequency that was associated with the tidal cycle. Both of these distributions were considered as mechanisms to maximise the success of nests.

High spring tides occasionally resulted in high nest losses of up to 69%, but the greatest overall threat to the nesting success was from the cattle that grazed the saltmarsh; these directly destroyed 45% of nests present. The nest losses due to predation were greater in 1979, a year of short vegetation, (25% of nests), than in the years of normal vegetation, when it was less than 4% of nests. In addition, within 1979 the predation was concentrated on the nests with little cover.

Nests that failed were usually replaced if there was sufficient time left in the breeding season. The interval between failure of one clutch, and the laying of the first egg of the next was usually 4 to 9 days.

All aspects of nest losses were considered and combined with the estimate of pullus production per successful nest, to

give several estimates of pullus production under different environmental conditions. These varied from 1.27 to 2.28 pulli per early nesting pair (including nest replacement), and from 0.73 to 1.72 pulli per late nesting pair (with no nest replacement).

7.2 THE ADULTS.

The adults captured at the nest were very difficult to sex because of their similar size and plumage, and the method used in this study relied on the constancy of mean egg volume of a female to identify some males (the 'M.E.V. method). From these males, and their mates, the size differences of the sexes were seen to be very slight. The validity of this sexing method was demonstrated by the correlation of egg size with maternal size, but not with paternal size. For some further analyses the sexing of all individuals was attempted with the following criteria (listed in order of decreasing reliability), M.E.V. method, cloaca width and weight. The size of members of pairs was not correlated, and it was assumed there was no selection of mate on this basis.

The timing of breeding within a season was mainly dependent on an individuals age, and to a slight extent its mate's age, but not on mate fidelity.

Nest site fidelity between years was very great for faithful pairs (median distance between nests, 42m.) and for males with new mates (55m.), but significantly less for females with new mates (137m.). It was also greater for old males than for young ones. These factors were important in consideration of the results of the capture-recapture analysis, and in analysing mate fidelity.

A general model of mate fidelity was developed that combined the estimates of annual mortality and the mate fidelity

of surviving males, that indicated that 71% of surviving pairs remained faithful between years. Faithfulness to a previous mate did, however, increase the chances of future mate fidelity, and resulted in several long periods of mate faithfulness. The assumptions of the capture-recapture method of Jolly (1965) were tested and the data seen to be appropiate to analyse by this method. The overall estimate of annual survival for both sexes was 0.77, and the population within the 1.04km^2 study area estimated at 200 pairs.

The distribution of this specific breeding population at other times of the year was seen to be very widespread, from N. England to Portugal, but the main concentration of reports was from S.W. England. There was no influence of body size on the position of these reports, but the amount of breeding plumage attained was correlated with the distance/latitude of the reports. This was tentatively interpreted as a reflection of the different temperatures or photoperiods experienced at these sites.

7.3 THE EGGS.

The usual clutch of four eggs took 4.5 days, from the laying of the first egg, to complete, and usually 26 days to incubate, giving a nesting period of 30.5 days.

The mean egg size (for example, internal volume, 20.6cm^3) was the largest so far described for this species, and this was considered to result from the close proximity of the rich food supply of the estuary.

The mean egg volume of clutches was positively correlated with the maternal size (wing, bill and tarsus), but not with the paternal size. Egg volume was not significantly different between

the clutches of the same female, both within and between years, but between females there was a large, significant variation. Within a clutch there was also a large variation of egg volume, and this was due to the significantly smaller volume of the last laid (fourth) egg.

The weight loss of eggs during incubation showed two phases; an initial slow decline of $0.0049 g.cm.^{-3}day^{-1}$ from 26 to 5 days before hatching, and a rapid decrease of $0.0187 g.cm.^{-3}day^{-1}$ up to hatching (which was associated with the hatching process). The mean total weight loss of eggs was 17.8% of the fresh weight.

Hatching of the clutch was often apparently sychronous, but when not the last laid egg tended to hatch later than the other three, possibly because incubation often began before the last egg was laid.

7.4 THE PULLI.

The size of pulli was estimated by three parameters, the length of the bill, the length of the tarsus and the weight. These enabled growth curves to be produced, mainly from pulli of known age.

The size at hatching was highly positively correlated with the size of the egg (especially the egg volume), and with the maternal size (especially the wing length). The mean size of pulli recently hatched was; bill length 10.94mm. (28% of mean adult size), tarsus length 26.83mm. (56%) and weight (13%) 16.45g.

After hatching there was a large weight loss of approximately 2.0g. (12% of mean hatching weight) in 36hrs., and the recovery of hatching weight occured after 70-80hrs. in many individuals. It then increased at about $5 g.day^{-1}$ until the age of fledging approached, when there was some levelling off. Both growth in bill length

($0.62mm.day^{-1}$) and tarsus length ($0.73mm.day^{-1}$) were roughly linear throughout the pre-fledging period, and bill length was considered most reliable as an estimator of age.

The mean relative growth rate of the pulli was considerably slower than that reported for five species of Arctic wader, and for Redshank in captivity. The difference was considered a reflection of the great abundance and availabilty of food for the Arctic and captive birds.

At 25 days old, near to fledging, the bill length and weight were less than 70% of the mean adult size, but the tarsus length was greater than 90%.

The postnatal moult is fully described, and shows that the cervical region of the dorsal tract was still downy and the flight feathers not yet fully grown near to the time of fledging.

The extreme elusiveness and mobility of the pulli precluded an estimation of pre-fledging mortality at this site, but a method, using the ageing criteria of this study, was suggested that might give general estimates. However, subjective assessment of the disappearance of known broods shortly after leaving the nest, combined with the large weight loss at this time, suggested that there was a critical period from 1 to 4 days after hatching that probably accounted for the major part of the pre-fledging mortality.

7.5 THE POPULATION DYNAMICS.

A tentative model of the production and mortality in the population was produced. It estimated the pre-fledging mortality at 0.67 and further highlighted the impact of the cattle on the population. Aspects of population regulation were discussed, but no firm conclusions were reached.

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Appendix 1 The Spatial Distribution Of Nests Found Annually Within The Restricted Area From 1974 to 1981.

The following 'number grids' show the quantity and position of nests found each year within the Restricted Area Grid (see Fig. 2.3). These are not density estimates, because many peripheral numbers are derived from fractions of hectares.

The total number of nests found within the area is also shown (n).

Appendix 1 (continued)

1974

n = 140

			0	0	1	1	0	1	
			2	3	0	5	1	0	0
		0	3	1	4	1	2	0	2	0
		0	0	0	4	4	0	2	1	0
		0	0	1	4	2	0	0	0	0
	0	0	0	0	4	3	0	0	0	0
	1	0	0	2	4	3	1	0	0	
0	1	0	4	1	3	1	2	0	0	
1	0	0	0	1	3	0	0	0	0	
2	1	0	1	4	0	0	0	1		
0	0	1	0	1	0	0	1	0		
1	2	5	2	3	0	2	0	0		
4	7	2	5	5	3	1	0			
			1	1	2	0				

1975

n = 165

			3	0	1	1	0	0	
			2	1	0	0	0	0	0
		0	0	2	5	0	1	1	2	0
		0	0	0	3	2	0	3	2	0
		0	0	4	3	3	2	0	0	0
	1	0	0	0	6	7	0	0	0	0
	0	0	0	6	2	1	0	0	0	
0	1	5	5	4	2	0	0	0	0	
1	1	0	0	0	0	1	0	0	0	
2	0	1	0	3	4	0	0	0		
1	0	1	3	0	0	1	5	0		
2	2	3	4	3	2	5	2	0		
1	4	4	3	6	5	1	1	0		
				1	2	4	2			

Appendix 1 (continued)

1976

n=169

			1	0	1	0	0	0	
			1	5	1	0	0	0	0
		0	0	2	7	2	0	0	2	0
		0	0	0	4	3	0	0	1	1
		0	0	0	3	3	2	0	0	0
	0	0	0	0	6	11	3	1	0	1
	1	5	1	4	5	1	1	0	0	
0	2	0	5	2	2	2	0	0	1	
0	1	0	0	0	0	1	0	0	0	0
1	1	0	0	0	4	5	1	0	0	
4	6	1	1	1	3	0	0	1	1	
1	2	0	2	5	4	4	5	2	0	
	0	4	3	0	4	2	2	1	0	
					1	1	1	0		

1977

n=164

			0	1	0	0	0	0	
			0	1	0	0	0	0	1
		0	0	0	3	3	0	1	3	2
		0	0	4	4	1	1	0	0	1
		0	0	2	4	2	2	3	0	0
	0	0	0	0	5	8	0	1	0	1
	0	0	0	6	2	4	1	2	0	
0	0	0	5	3	2	1	1	3	0	
0	0	0	0	0	0	0	1	1	0	0
0	0	0	0	0	0	0	0	0	1	
3	5	1	0	0	0	0	1	6	0	
0	1	2	2	2	2	6	10	10	0	
	0	2	4	8	7	2	0	0	1	
					1	0	1	0		

1978

n=147

				0	2	2	0	0	0	
				1	1	0	0	0	0	4
			0	0	1	2	0	0	0	2	2
			0	0	1	5	2	0	0	0	2
			0	0	2	5	0	2	0	0	2
		0	0	0	1	17	7	0	0	0	0
		0	1	4	2	3	7	2	0	0	
	0	0	0	0	2	0	0	0	0	0	
0	0	0	0	0	0	0	1	0	0	0	
0	1	0	0	0	1	1	0	0	1		
3	2	0	1	1	2	0	0	0	0		
0	0	0	3	2	0	5	6	3	0		
	1	2	6	5	6	3	1	1	0		
					1	1	2	1			

1979

n=145

				3	1	0	0	0	2	
				0	3	1	0	0	1	4
			0	0	3	4	0	0	0	0	1
			0	0	4	4	0	0	0	1	9
			0	0	3	7	1	0	0	0	1
		0	0	0	0	6	4	0	0	0	0
		0	0	0	3	6	4	2	1	0	
	0	1	1	1	1	3	1	1	0	0	
0	0	0	0	0	1	0	0	0	0	0	
0	0	0	0	0	1	2	0	0	1		
0	0	0	0	0	0	0	0	1	0		
0	1	1	4	4	3	9	6	3	0		
	2	2	5	4	4	3	0	0	0		
					0	0	0	0			

1980

n=127

			2	1	1	0	0	1	
			0	3	1	0	0	1	0
		0	0	1	1	0	1	0	2	1
		0	0	0	3	1	0	1	1	3
		1	0	1	6	1	2	2	0	1
	0	0	0	0	5	8	1	1	0	0
	0	0	2	1	3	0	1	0	0	
0	2	0	2	3	2	1	1	0	0	
0	1	0	0	1	0	0	0	1	0	0
0	0	0	1	0	0	1	1	0	1	
0	0	0	3	2	0	0	0	1	2	
0	0	1	2	4	4	4	4	0	0	
	0	2	1	2	1	9	3	0	0	
					0	2	1	0		

1981

n=173

			1	0	0	0	0	1	
			1	1	0	0	1	3	4
		0	0	1	1	2	0	0	0	1
		0	0	2	3	0	0	1	1	2
		0	0	1	4	0	1	1	0	1
	0	1	0	0	6	8	4	2	0	0
	0	0	1	2	5	10	2	0	0	
0	0	0	0	1	1	3	5	0	1	0
0	0	1	0	0	0	0	1	1	0	0
0	0	0	0	0	1	0	0	0	1	
0	1	1	1	0	0	0	0	1	2	
0	2	1	4	3	4	2	7	4	0	
	0	1	2	6	14	12	4	0	0	
					6	2	2	0		

APPENDIX 2 The Index Of Dispersion.

The Poisson series describes a random distribution, such that one individual does not influence the distribution of another, and the mean number ($\bar{x}$) of individuals is equal to the variance (S^2) of the samples (N). This fact provides a test of significance of agreement with the Poisson distribution, in that the ratio of $\bar{x}$ and S^2 can be tested by chi - squared, X^2;

$$X^2 = \frac{(N-1)\ S^2}{\bar{x}} \qquad \text{(with N-1 df.)}$$

(For further details see Southwood (1966), or Steele and Torrie (1980)).

Closely related to this, is the Index of Dispersion, (I.D.), which describes the departure of a distribution from randomness;

$$\text{I.D.} = \frac{X^2}{N-1}$$

$$= \frac{S^2}{\bar{x}}$$

If the X^2 does not differ significantly from 1, the distribution is not different from the Poisson, and is therefore random.

If the X^2 does differ significantly from 1, the distribution can be of two types;

a) I.D. greater than 1 implies an aggregated distribution.

b) I.D. less than 1 implies a regular distribution.

APPENDIX 3 The Mayfield (1975) Method Of Estimating Nest Losses.

Observed losses depend on the number of nests in the sample, and the amount of time each nest was observed, that is exposure, in nest days. With daily visits to each nest, the estimation of exposure presented no problems. However, if there was an interval of more than one day, and a nest loss was observed, it was presumed to have occured mid way between visits, such that exposure was half the interval.

$$\text{Nest mortality, } m = \frac{\text{losses}}{\text{exposure}} \quad \text{nests.day}^{-1}$$

Therefore, the daily survival rate, s, was;

$$s = 1 - m \quad \text{nests.day}^{-1}$$

With a nesting period of t days, the probability of a nest surviving the entire nesting period was;

$$P(\text{surviving nesting period}) = s^t$$

The standard error of s, $S.E._s$, was derived by Johnson (1979);

$$S.E._s = \sqrt{\frac{(\text{exposure} - \text{losses}) \times \text{losses}}{(\text{exposure})^3}}$$

and, 95% confidence limits for s were calculated as;

$$s \pm 1.96 \times S.E._s$$

Appendix 4 The Analysis Of Variance Of Adult Measurements.

WEIGHT (g.)

Source	df.	SS	MS	F
Among birds	24	6863.55	285.98	7.44
Within birds	100	3842.40	38.42	
Total	124	10705.95		

$P < 0.001$

mean = 132.13

SE = 2.78

95% confidence limits = ± 7.70

CV = 4.69%

**1 Percent variance among birds = 56.3%

Percent variance within birds = 43.7%

WING LENGTH (mm.)

Source	df.	SS	MS	F
Among birds	24	1027.7	42.82	18.55
Within birds	100	230.8	2.31	
Total	124	1258.5		

$P < 0.001$

mean = 167.65

SE = 0.68

95% confidence limits = ± 1.89

CV = 0.9%

Percent variance among birds = 77.8%

Percent variance within birds = 22.2%

**1 Percent variance among birds is also termed the coefficient of interclass correlation (see Sokal & Rohlf 1969, p.211)

BILL LENGTH (mm.)

Source	df.	SS	MS	F
Among birds	23	364.59	15.85	16.36
Within birds	96	93.00	0.97	
Total	119	457.59		

$P < 0.001$

mean = 41.89

SE = 0.44

95% confidence limits = ± 1.22

CV = 2.35%

Percent variance among birds = 75.4%

Percent variance within birds = 24.6%

TARSUS LENGTH (mm.)

Source	df.	SS	MS	F
Among birds	24	456.71	19.03	14.10
Within birds	100	135.10	1.35	
Total	124	591.81		

$P < 0.001$

mean = 48.74

SE = 0.52

95% confidence limits = ± 1.44

CV = 2.38%

Percent variance among birds = 72.4%

Percent variance within birds = 27.6%

TARSUS WIDTH (mm.)

Source	df.	SS	MS	F
Among birds	22	0.838	0.0381	9.45
Within birds	92	0.371	0.0040	
Total	114	1.209		

P < 0.001

mean = 2.412

SE = 0.028

95% confidence limits = ± 0.079

CV = 2.6%

Percent variance among birds = 63.0%

Percent variance within birds = 37.0%

TAIL LENGTH (mm.)

Source	df.	SS	MS	F
Among birds	24	323.26	13.47	1.10
Within birds	100	1218.79	12.19	
Total	124	1542.05		

P > 0.1

mean = 65.83

SE = 2.44

95% confidence limits = ± 6.77

CV = 5.3%

Percent variance among birds = 2.1%

Percent variance within birds = 97.9%

Appendix 5 Reports Of Adults Outside Of The Breeding Season.

The following three pages of tables identify the birds reported from July to March that were notified before November 1981. The distance from the breeding site is also given and this is visually presented on three maps. On these maps arrows indicate the position of the site, the letter identifies it (in the table), and the figure is the number of reports at that site.

Birds DR36229 (site i), DR13892 (site p), DR36243 (site v), DR21711 (site t) and another (not specifically identified but distinctive, at site A) were reported in different winters at the same site. There were no contradictions to this, therefore, the Redshank is very faithful to its wintering site aswell as its breeding site.

Appendix 5 (continued)

Site Code	No. of Reports	Locality.	Distance From Breeding Site (km.)	Date	Bird
aa	1	Arnside, Cumbria. 54 11'N 02 51'W	55	18-4-77	DR25120
a	1	Hest Bank, Lancs. 54 05'N 02 50'W	43	5-11-72	DS89375
b	1	Lancaster, Lancs. 54 02'N 02 49'W	37	23-8-80	DR52611**
c	2	Preesall, Lancs. 53 55'N 03 00'W	26	1-8-80	2 CM. birds together.**
d	1	Warton, Lancs. 53 44'N 02 55'W	3	26-12-77	DR36327
e	1	Lytham, Lancs. 53 44'N 02 56'W	4	20-2-77	DR25040
f	2	Southport, Merseyside. 53 38'N 03 01'W	4	11-3-78	DR51207
				29-1-76	DR25054
g	1	Chorley, Lancs. 53 39'N 02 44'W	22	27-12-76	DR36225
h	2	Point of Ayr, Clwyd. 53 21'N 03 19'W	47	31-7-77	DR13797
				31-7-77	DA33458
i	3	Moreton, Merseyside 53 24'N 03 07'W	36	4-11-78	DR22706
				4-11-78	DR36229
				7-9-80	DR36229**
j	1	New Brighton, Merseyside. 53 24'N 03 07'W	32	11-2-68	CR30106
k	1	Widnes, Cheshire. 53 22'N 02 44'W	44	17-10-77	DR36473
l	2	Beaumaris, Gwynedd. 53 15'N 04 03'W	90	23-11-80	DR52618**
				25-1-81	1 CM.**
m	1	Bardsey Island, Gwynedd. 52 46'N 04 48'W	161	25-9-79	DR97427
n	1	Swansea, West Glamorgan. 51 40'N 04 03'W	238	20-9-80	DR36246
o	1	Newport, Gwent. 51 34'N 02 48'W	244	2-12-78	DR11710
p	2	Lydney, Gloucester. 51 43'N 02 33'W	220	23-12-72	DR13892
				13-8-75	DR13892

Appendix 5 (continued)

q	3	Clevedon, Avon.	253	25-11-78	DR13714
		51 25'N 02 53'W		30-11-78	DR52603
				2-3-80	DR67662
r	1	Brean Down, Somerset.	275	12-2-78	DR13802
		51 19'N 03 00'W			
s	3	Taw/Torridge Est.,Devon.	311	October-80	3 CM.**
		51 05'N 04 15'W		possibly only 1 bird	
t	3	Camel Estuary, Cornwall.	375	26-7-75	DR21711
		50 32'N 04 50'W		25-8-80	DR21711
				28-8-77	DR36484
u	1	Fal Estuary, Cornwall.	424	28-12-80	DR13843
		50 10'N 05 05'W			
v	6	Plym Estuary, Devon.	383	16-12-77	DR36243
		50 22'N 04 07'W		5-1-78	DR36243
				20-8-78	DR52655
				21-1-81	1 CM.**
				11-3-81	1 CM.**
				13-8-81	1 CM.**
w	1	Kingsbridge, Devon.	398	31-7-80	1 CM.
		50 15'N 03 45'W			
x	7	Portsmouth, Hampshire.	343	8-11-73	DS52229
		50 50'N 01 03'W		23-8-78	DR13770
				8-3-78	DR25034
				8-3-81	DR36212**
				8-3-81	DR36495**
				21-8-81	1 CM.**
				Sept.-81	DR36450**
y	1	Pagham Harbour, Sussex.	368	9-11-80	DR36215**
		50 45'N 00 45'W			
z	1	Pegwell Bay, Kent.	388	10-8-71	DR36319
		51 20'N 01 25'E			

Appendix 5 (continued)

Site Code	No. of Reports	Locality.	Distance From Breeding Site (km.)	Date	Bird
A	x[1]	Jersey, Channel Isles.	505	25-8-81	DR52668**
		49 10'N 02 02'W		7-9-81	DR52668**
B	1	Harfleur, France.	519	31-7-80	DR97332[2]
		49 30'N 00 22'E			
C	1	Baie de Morlaix, France.	580	20-1-81	1 CM.**
		48 35'N 03 50'W			
D	1	Cotes - du - Nord, France.	561	22-1-78	DR36222
		48 48'N 03 25'W			
E	2	Finistere, France.	669	27-7-75	DR25032
		47 49'N 04 20'W		30-10-77	DR25091
F	1	Chaillevette, France.	918	6-12-75	DR25049
		45 44'N 01 03'W			
G	1	Oporto, Portugal.	1488	20-9-78	DR36365
		41 07'N 08 35'W			

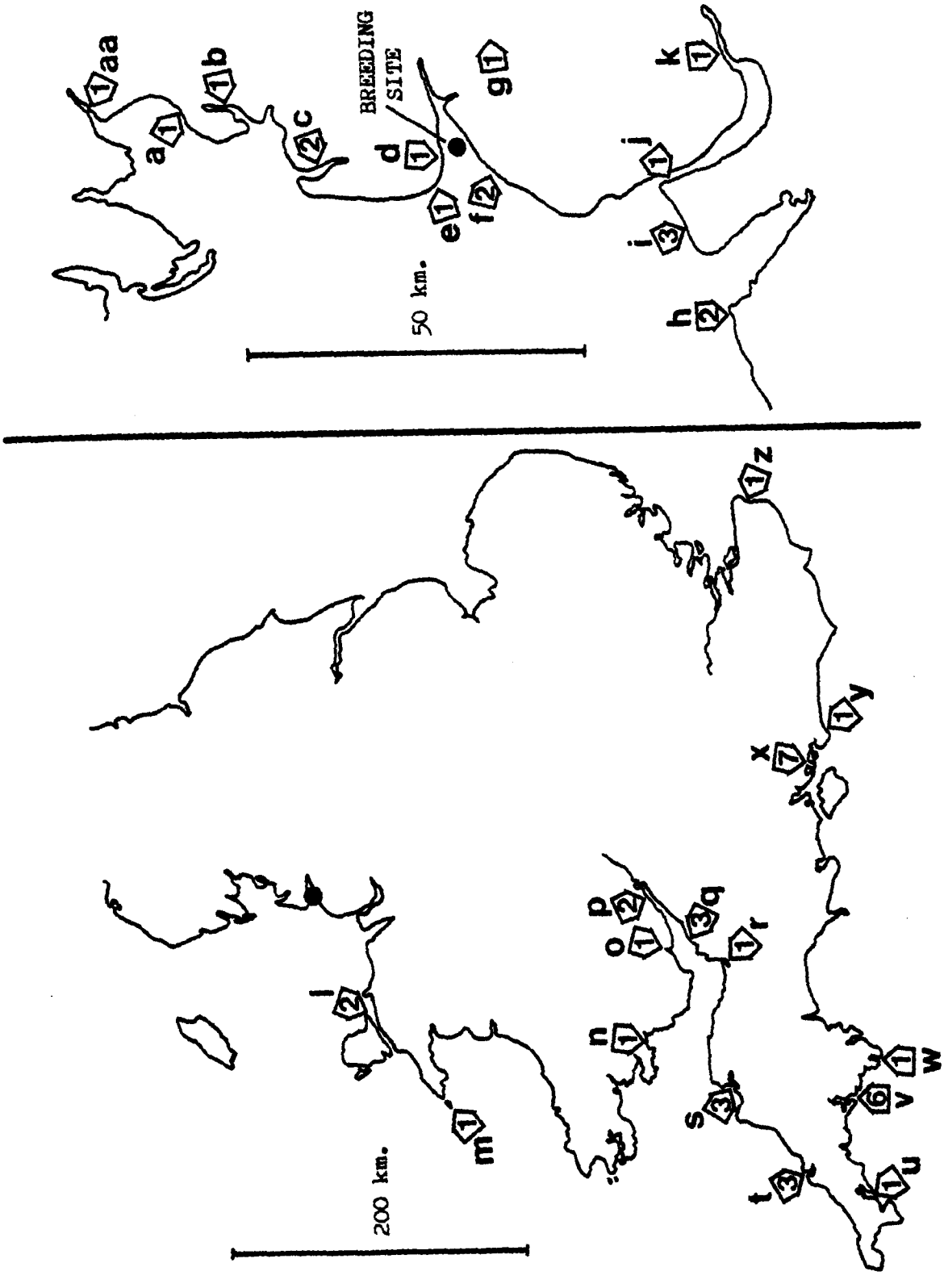
Notes.

1) all reports from Jersey came from one observer, who noted many birds throughout the period from August to November. Only the individual in the table, above, was positively identified.

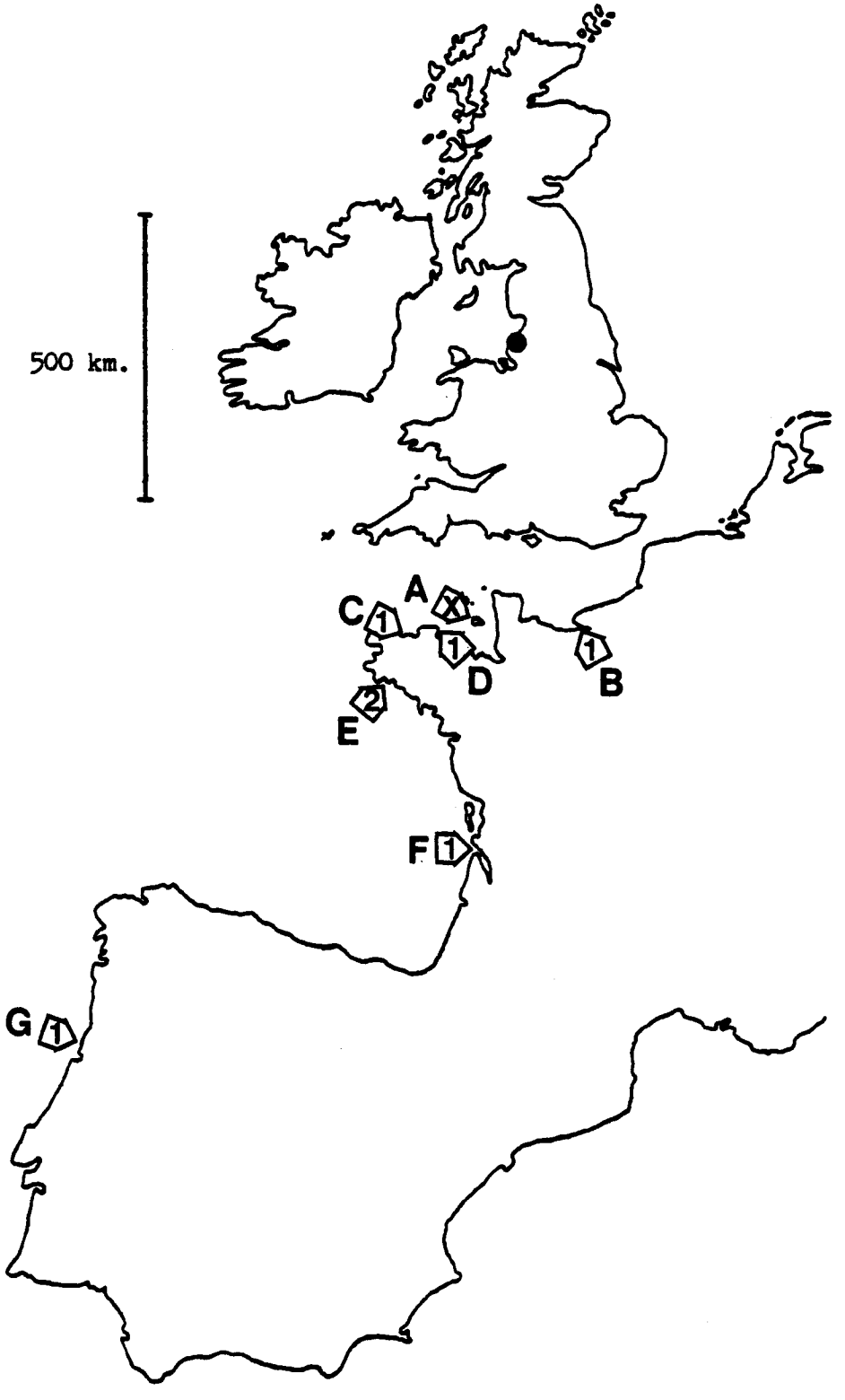
2) this bird was shot only 67 days after hatching.

** identification by patagial wing tags.

Appendix 5 (continued)



Appendix 5 (continued)



Appendix 6 . The Effect On Mate And Nest Site Fidelity Of Desertion Because Of Trapping.

It is desirable to consider any effect of nest 'trapping losses' on both nest site and mate fidelity, because this was a potential deviation from a natural state, which may affect the interpretation of the results of Sections 3.3.5 and 3.3.6. As in these sections, the individuals captured within pairs in consecutive years are considered for faithfulness to the initial years mate and nest site. Comparisons are made of initial nests deserted because of trapping, and those with more natural outcomes (that is, all other classifications of nest outcome).

The low frequency of pairs from initial nests deserted because of trapping determines that the chi-square analysis is by the Fisher's exact method.

Mate Fidelity.

	Males		Females	
	Faithful	Unfaithful	Faithful	Unfaithful
Natural outcome.	26	26	26	17
Trapping loss.	2	8	2	2
Fisher's exact prob.	= 0.134		= 0.362	

For both sexes there was no significant effect on mate fidelity of nest loss due to trapping.

Nest Site Fidelity.

The distance between nest sites is considered with respect to the median distance of the sex and mate fidelity groups (see Fig.3.7).

	Males		Females	
	∠ median	< median	∠ median	< median
Natural outcome.	27	25	21	22
Trapping loss.	2	6	1	3
Fisher's exact prob.	= 0.394		= 0.286	

For both sexes there was no significant effect on nest site fidelity of nest loss due to trapping.

The limited data available therefore suggests that the results of Sections 3.3.5 and 3.3.6 were not influenced by the desertion of nests due to trapping.